

AGRIOTHERIUM (MAMMALIA, URSIDAE) FROM LANGEBAANWEG, SOUTH AFRICA, AND RELATIONSHIPS OF THE GENUS

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(With 42 figures and 21 tables)

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ABSTRACT

Agriotherium africanum from the latest Miocene/early Pliocene Varswater Formation at Langebaanweg, and other relevant material indicate that *Agriotherium* was descended from late Miocene *Indarctos*. Later Ursidae are divided into the subfamilies Ursavinae (*Ursavus* spp), Agriotheriinae (tribes Agriotheriini and Ailuropodini), and Ursinae (Ursini and Tremarctini). '*Ursavus*' *depereti* and *Ailuropoda melanoleuca* constitute the Ailuropodini, and *Indarctos* and *Agriotherium* the Agriotheriini. The latter consist of a primary European lineage from which branches in Africa, Asia and North America arose. Either all species of *Indarctos*, or the later ones only, should perhaps be referred to *Agriotherium*.

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INTRODUCTION

Agriotherium africanum from the latest Miocene/early Pliocene Varswater Formation exposed in a phosphate mine ('E' Quarry) at Langebaanweg, Cape Province (Fig. 1), was the first member of its genus to be recorded in Africa, and the first bear known from sub-Saharan Africa (Hendey 1972; Wolff *et al.* 1973). Although the first *Agriotherium* specimens were found in Europe at least as long ago as 1809 (Stehlin 1907), and others have since been collected at scattered localities through much of the Old World and North America, this genus has remained relatively poorly known, being represented for the most part by fragmentary material belonging to few individuals.

Initially this also applied to the Langebaanweg representative of the genus, but later more material came to light and it is remarkable that '*Agriotherium africanum*, the most recently described and most remote record of the genus, is apparently also the best represented' (Hendey 1977: 112). It is in the latter

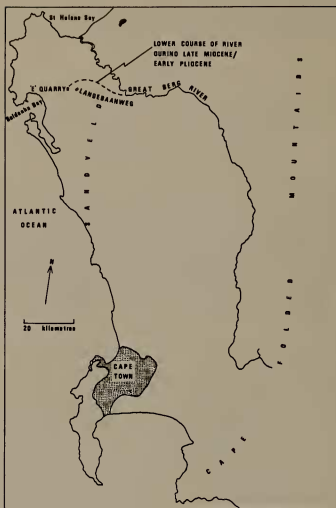


Fig. 1. The south-western Cape Province.

respect that *A. africanum* is particularly noteworthy. It provides the best indication yet that *Agriotherium*, like other bears, was characterized by appreciable variation in its dentition and in size, the latter evidently being due to marked sexual dimorphism.

A. africanum specimens are recorded from two stratigraphic horizons in 'E' Quarry, namely beds 3aS and 3aN of the Pelletal Phosphorite Member (Hendey 1976). The bed 3aS sample, which includes the holotype, comprises only a small part of the total assemblage. Most of the bed 3aN sample was collected in a restricted area (the fossil accumulation at Locality 5—Dingle *et al.* 1979, fig. 2). This material is from a river channel lag deposit, which was laid down in the lee of a phosphate rock outcrop, while the remainder of the bed 3aN sample was from lateral extensions of the lag deposit. Since this material was probably accumulated during a very restricted period, the bed 3aN

A. africanum sample may represent remnants of a single population in a temporal as well as a geographical sense. There is no reason to believe that the character diversity observed in this sample can be ascribed to anything but normal intra-specific variation.

On the other hand, there are differences between bed 3aS and bed 3aN specimens which apparently reflect evolutionary changes, suggesting that the time interval between deposition of these beds was of sufficient duration for such changes to have occurred. The differences are, however, insufficient to warrant formal nomenclatural recognition. *A. africanum* thus joins the growing number of species which indicate that deposition of the Varswater Formation took place over an appreciable period in time (see Hendey 1978; Gentry 1980). Langebaanweg is the only recorded locality where *Agriotherium* is known to occur in more than one stratigraphic horizon.

A. africanum is also of interest since it is one of several species now known from sub-Saharan Africa which indicate that towards the end of the Miocene this region had closer faunal links with Eurasia (Hendey 1978). The present study of *Agriotherium* has suggested that faunal interchange at this time was between Africa and Europe, presumably by way of an Iberian/north-west African connection, rather than, or in addition to, one between Africa and Asia via the Middle East. Apart from *A. africanum*, the Langebaanweg carnivores, *Plesiogulo monspessulanus* and *Dinofelis diastemata*, also point to such a connection, as have recent studies on other mammals (e.g. Forstén 1978).

Until the recent discovery of an agriotheriine at Sahabi in Libya (Boaz *et al.* 1979), the Langebaanweg *Agriotherium* was the only African record of the group, and its location at the southern continental extremity was evidence that it had been widespread on this continent.

On a more mundane level, *A. africanum* has an appeal in that it is still South Africa's only known bear, living or fossil.

The material described below is housed in the South African Museum, and catalogue numbers are prefixed SAM-PQ-, which identifies the institution and department concerned. This lettering is omitted from the text, and the locality prefix (L) and serial numbers of specimens only are given. Modern comparative material in this museum is distinguished by the prefix ZM.

Other institutional abbreviations used in the text are as follows:

BMNH—British Museum (Natural History), London

GSI —Geological Survey of India, Calcutta

NMB —Naturhistorisches Museum, Basel

NMW —Naturhistorisches Museum, Vienna

Originals and casts of *Agriotherium* and related taxa in, or from, the above institutions were examined in the course of the present study. In addition, skulls and skeletons of extant ursids in the South African Museum and the British Museum (Natural History) were studied. Comparative data were otherwise obtained from the publications cited.

THE LANGEBAANWEG *AGRIOTHERIUM*

MATERIAL

The available *Agriotherium africanum* specimens are listed below according to the horizon from which they were derived, and, where possible, according to sites or areas within 'E' Quarry.

Pelletal Phosphorite Member, bed 3aS

- L2045—Left maxillary fragment with P⁴ (holotype)
- L1868—Left I₁, right P³, fragments of right P⁴ and M¹
- L1844, L3141—Left I₂ and I₃, probably of the same individual (Wolff *et al.* (1973) were incorrect in identifying L1844 as a right I₁)
- L12637—Incomplete left M¹ (Hendey (1972) was incorrect in identifying this tooth as M²)
- L2154—Incomplete proximal left ulna

The above specimens were described or discussed by Hendey (1972) and Wolff *et al.* (1973).

- L12561—Right M₃ (see Hendey 1972)
- L12033, L41270—Right I³'s
- L40031—Left hemimandible fragment and distal left humerus
- L40030—Right metatarsal II and 2nd phalanx, probably of same individual as L40031
- L40002—Left femur and patella, and a thoracic vertebra, of one individual
- L3433—Left humerus lacking proximal parts
- L3994—Shaft of left humerus
- L40040—Distal right humerus
- L12383—Proximal right ulna
- L40003—Left radius lacking distal parts
- L41702—Left scapholunar
- L41295—Right cuneiform
- L12503—Right pisiform
- L20998, L25862—Right metacarpals III
- L41575—Right metacarpal IV
- L40043, L40128—Proximal right and left femora
- L40028, L40029—Proximal right tibiae
- L41108—Proximal right metatarsal V
- L10411—Proximal 1st phalanx
- L42667—2nd phalanx

The above material represents at least three individuals, but since the specimens were collected over a wide area and from different levels within bed 3aS, the actual number is certainly much higher. Unless otherwise stated, each catalogue number could represent a different individual, which makes a total of 28.

It is not certain that those specimens in this series with numbers above L40000 are all from bed 3aS (see p. 62).

Pelletal Phosphorite Member, bed 3aN—excavation LBW-E 1975/1 (site—TCWW Prom)

L33160—Incomplete left manus, comprising scapholunar, unciform, magnum, trapezoid and metacarpals II to V, the latter lacking distal ends and some of the carpals incomplete

L33341, L34188—Incomplete right and left innominates

L30205—Left metatarsal III

L33557—Proximal left metatarsal V

The above material represents at least 2 individuals.

Pelletal Phosphorite Member, bed 3aN—excavation LBW-E 1976/1 (site—RP)

L33824—Crown of left \underline{C} .

L33825—Left I_3

L13826—Proximal right radius

L33828—Right metacarpal IV

L33830—Distal metapodial fragment

The above material represents at least one individual.

Pelletal Phosphorite Member, bed 3aN—excavation LBW-E 1976/2 (site—IWRP or Locality 5 of Dingle et al. 1979)

L45062—Incomplete skull (partly restored) and mandible (restored), lacking left I^1 , right I^3 , left and right P^1 , right lower incisors, and left P_3

Associated postcranial bones, including: parts of at least 7 vertebrae (some numbered L49048 and L49115); fragment of distal right humerus; right ulna lacking distal parts; right scapholunar, cuneiform, pisiform, unciform, magnum and trapezoid; proximal right metacarpal III; proximal left humerus; left ulna with distal parts detached and fragmented; left radius lacking part of shaft; right tibia and proximal fibula; right astragalus, calcaneum, navicular and cuboid; right metatarsals II, IV and V; left astragalus; left metatarsal III and proximal metatarsal II; 11 sesamoids, five 1st phalanges, four 2nd phalanges and four 3rd phalanges

L45137—Right I^2 , \underline{C} lacking root, and P^4 to M^2 ; left \underline{C} and P^4 to M^2 ; some skull fragments

L45114—Right hemimandible lacking ascending ramus, incisors, P_3 and M_3

The above specimens were briefly discussed by Hendey (1977).

L46605, L48564, L48577—Left and right maxillary fragments with M^2 's and part of left M^1

L46573—Crown of right I^2

L47758/9—Right and left I^3 , probably of the same individual

L48851—Fragment of left I^3

L46074—Right P^4

L47698—Left M^2

L46563—Left M_2 , probably of same individual as L45114

L48742—Fragment of mandibular condyle

- L47449, L47701, L47830—Incomplete cervical vertebrae
 L45063—Incomplete left forelimb, comprising humerus (partly restored), with proximal end detached; ulna and radius (restored); scapholunar, cuneiform, pisiform, unciform, magnum, trapezoid and trapezium; metacarpal, V, and fragments of metacarpals I, III and IV; three sesamoids; three 1st phalanges
 L46602—Proximal left humerus
 L48741, L48747—Proximal left radii
 L47699/700—Proximal left and right radii of one individual
 L46076—Right ulna lacking distal end
 L46134—Left scapholunar, right pisiform and metapodial fragment, probably of one individual
 L46132, L48021—Left and right scapholunars
 L47074—Right magnum
 L45448—Left metacarpal I and distal metapodial fragment, probably of one individual
 L48432—Right metacarpal IV
 L49889—Distal left femur
 L47533, L47910—Left and right astragali
 L47387—Proximal right metatarsal I
 L48572/3—Right metatarsal V and left metatarsal II, probably of one individual
 L46133, L46216, L48766—Metapodial fragments
 L47358, L48533, L48730, L49888—1st phalanges
 L48213, L48230—2nd phalanges

The above material represents at least five individuals.

Pelletal Phosphorite Member, bed 3aN—surface finds in the vicinity of LBW-E 1976/2

- L47242—Left premaxilla and right M² of one individual.
 L50636—Right I³
 L50981—Left M₃
 L42537—Proximal left ulna and distal femur, lacking epiphyses, of one individual
 L50635—Left scapholunar
 L50638—Patella
 L50637—Distal metapodial
 L41468—1st phalanx

The above material represents at least two individuals.

Pelletal Phosphorite Member, bed 3aN—dump 10 sample from deposits immediately north of LBW-E 1976/2

- L55012—Left and right P⁴'s and right M¹ of one individual
 L55015, L55016—Right I²'s
 L55014—Left I³

- L55013—Crown of right \bar{C}
- L55017—Four anterior premolars of more than one individual
- L55029—Right metacarpal I
- L55019—Distal left fibula
- L55021—Right navicular
- L55022/28—Seven metapodial fragments
- L55020—Sesamoid
- L55030/35—Six 1st phalanges
- L55036—2nd phalanx
- L55037/43—Seven 3rd phalanges

The above material represents at least two individuals.

Pelletal Phosphorite Member, bed 3aN—dump 9 sample from deposits immediately west of LBW-E 1976/2

- L50445—Incomplete left hemimandible with \bar{C} and P_4
- L50453—Fragment of left P^4
- L50458—Right I_2
- L50446—Right M_1
- L50457—Left magnum
- L50454—Distal metapodial fragment
- L51592—2nd phalanx
- L50455/6—Two 3rd phalanges

The above material represents at least one individual.

Pelletal Phosphorite Member, bed 3aN—dump 8 sample from deposits immediately south of LBW-E 1976/2

- L50003—Incomplete left hemimandible with P_4 and M_2
- L50004—Incomplete left hemimandible with P_4 and associated M_1 and M_2
- L50903—Fragments of right hemimandible with incomplete \bar{C}
- L50008—Incomplete right P^4
- L50005/6—Right and left M_1 's
- L50007—Right M_2

Unnumbered teeth and tooth fragments, including right I^2 , I^3 and I_1 , a canine and two anterior premolars

- L50843/54—Eleven vertebra fragments
- L50857/8—Incomplete left and right scapulae
- L50834/5/6/8/9—Humerii fragments of at least two individuals
- L50806, L50816—Proximal left and right radii
- L50807—Distal right radius fragment
- L50777—Distal epiphysis of right radius
- L50763—Left ulna lacking distal end
- L50764—Left ulna fragment
- L50840—Proximal ulna fragment

- L50805, L50808—Distal right ulnae
 L50767—Right scapholunar
 L50813, L50819—Fragments of right and left scapholunars, probably of one individual
 L50786, L50795—Left and right cuneiforms
 L50772, L50774—Right unciforms
 L50791, L50794—Right magnums
 L50775—Left metacarpal I
 L50783, L50788—Left and right metacarpals III
 L50810—Proximal right metacarpal III
 L50855/6/9/60—Femora fragments of at least two individuals
 L50841, L50833—Proximal and distal left tibia, probably of one individual
 L50842—Proximal right tibia
 L50769—Distal epiphysis of right tibia
 L50815, L50828—Distal left and right fibulae
 L50765/6—Left astragali
 L50770, L50789—Right astragali
 L50768—Right calcaneum lacking tuber calcis epiphysis
 L50773—Left navicular
 L50778, L50790—Right and left entocuneiforms
 L50771, L50787—Left and right metatarsals I
 L50824—Proximal left metatarsal IV
 L50812, L50829—Proximal right metatarsals V
 L50809/11/14/17/18/20/22/23/25/26/30—Eleven metapodial fragments
 L50802—Sesamoid
 L50776/80/81/84/93/97—Six 1st phalanges
 L50821/7—Two incomplete 1st phalanges
 L50785/96/804—Three 2nd phalanges
 L50782/98/99/800/801—Five 3rd phalanges
 L50831—Incomplete 3rd phalanx

The above material represents at least four individuals.

Pelletal Phosphorite Member, bed 3aN—carbonaceous deposit south of dump 8 area

- L41404—Fragmented and incomplete skull, with only the left premaxilla and maxilla largely intact, and with right ?P², and left C (damaged), P⁴, M¹ and M² (see Hendey 1977)
 L40044—Mandible fragment with associated right radius and fragments of ulna
 L43126—Fragments of at least six thoracic and lumbar vertebrae.

The above material represents at least two individuals.

The minimum number of individuals represented in the combined bed 3aN samples is eleven, although the actual number may be far higher. These samples are from a single horizon of river channel and associated deposits, which were exposed over a linear distance of about 200 m, with sample areas either contiguous

or not far removed from one another. Elements of individual skeletons are likely to be represented in more than one sample unit.

THE SKULL

Apart from L45062, the only other described skull of *Agriotherium* is one belonging to *A. sivalense* from the Siwalik Hills in India (Falconer & Cautley 1836; Lydekker 1884). Both skulls are incomplete, and although L45062 is also slightly distorted in parts, it is perhaps the more informative of the two specimens. They are similar in overall size, and, in so far as comparisons are possible, they are also similar in morphology.

Another skull which is remarkably like that of the Langebaanweg *Agriotherium* is of an *Indarctos* from Florida which was recently described by Wolff (1978). Although the Langebaanweg and Florida skulls undoubtedly do belong to *Agriotherium* and *Indarctos* as these genera are presently conceived, the description of skull characters in the latter (Wolff 1978: 2-4) could, with only slight modification, serve as a description of the Langebaanweg specimen. The significance of this will be discussed later (see p. 93).

Other described skulls of *Indarctos*, of which there are two from Samos (Helbing 1932; Thenius 1949, 1959) and one from Spain (Crusafont & Kurtén 1976), are less like the Langebaanweg specimen because they represent species which are more primitive than that from Florida.

A summary account of the skull characters of L45062 has been given elsewhere (Hendey 1977), but they are dealt with in more detail here.

The skull of *A. africanum* (Fig. 2) differs in certain aspects from those of all living bears. Its most striking characteristic is its massive size (Table 1), although in some dimensions it is matched, or even surpassed, by skulls of male Kodiak bears (*Ursus arctos middendorffi*), which are amongst the largest of living bears (Hendey 1977, table 1). *A. africanum* is otherwise most readily distinguished from living bears by its relatively short and broad snout, while the braincase, which is surmounted by a very high sagittal crest, appears small by comparison. The nuchal crest is also very prominent and dorsally projects well behind the occipital condyles. The zygomatic arches are very stout and strongly arched. They resemble those of the giant panda, *Ailuropoda melanoleuca*, more than any other living ursid, and, amongst extinct ursids in which the zygomata are known, they are closest to those of the Florida *Indarctos* and North American *Arctodus simus* (Kurtén 1967).

In all these respects the skull of *A. africanum* is reminiscent of that of the lion, *Panthera leo*, although the latter is far smaller, and, of course, very different in detail (Fig. 3). The resemblances between the skulls of *Agriotherium* and *P. leo* are probably due to their sharing adaptations to a carnivorous way of life.

By curious contrast, the *A. africanum* skull also resembles that of the most herbivorous of all bears, *Ailuropoda*, as well as that of *Indarctos*, another supposed herbivore (Wolff 1978). This may be an indication that the actual nature of the diet is less important than the requirement in certain Carnivora

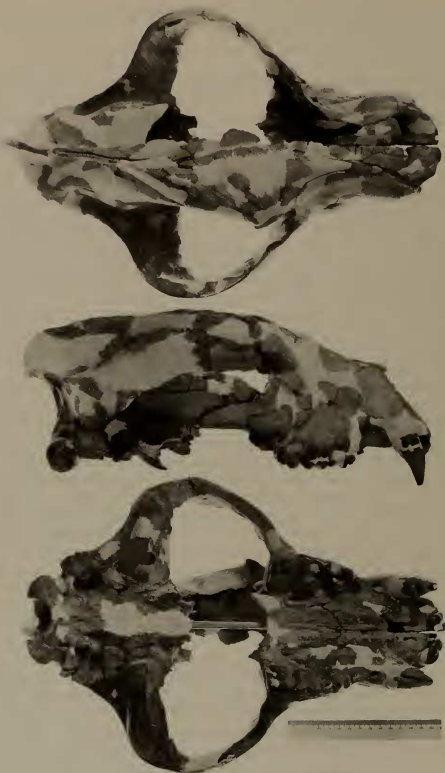


Fig. 2. Dorsal, lateral and ventral views of the Langebaanweg *Agriotherium* skull, L45062.

TABLE 1

Dimensions of Langebaanweg *Agriotherium* skull and mandible.

SKULL	L45062	L41404		
Basal length	c. 381,0	—		
Condylobasal length	c. 420,0	—		
Palate length (posterior alveolar margin of P's to posterior palatine incisure)	c. 165,0	—		
Zygomatic width	c. 305,0	—		
Rostral width (over <u>C</u> 's)	c. 118,0	—		
Width over M ² 's	135,0	—		
Interorbital width	c. 125,0	—		
Width over postorbital processes	c. 150,0	—		
Occiput width at base of mastoid processes	c. 130,0	—		
Condylar width	c. 90,0	—		
<u>C</u> -M ² length at alveolar margin	149,0	154,0		
P ⁴ -M ² length at alveolar margin	83,5	82,5		
MANDIBLE	L45062	L45114	L50003	L50004
Length (<u>C</u> to condyle)	296,0	—	—	—
Height of ascending ramus	142,0	—	—	—
Transverse diameter of condyle	71,0	—	—	—
Depth below M ₁	69,0	68,5	c. 74,0	—
Breadth below M ₁	26,9	26,8	24,7	—
Depth at diastema	61,0	66,0	65,3	59,4
C-M ₃ length at alveolar margin	174,0	c. 190,0	c. 190,0	—
P ₄ -M ₃ length at alveolar margin	104,0	c. 117,0	111,0	—

for unusually powerful jaw musculature, with consequent similar modification of the masticatory apparatus.

There are also some similarities between the skulls of *A. africanum* and the polar bear, *Thalarctos maritimus*, which is the most carnivorous of living Ursinae. Like *A. africanum*, *Thalarctos* also has a relatively broad snout and a relatively straight dorsal profile in lateral view. These, and other, resemblances between *Thalarctos* and *A. africanum* will be discussed again later.

Although *Thalarctos* has a relatively broad snout, it is simply a modification of the 'long-faced' ursine condition, and it is easily distinguished from 'short-faced' Tremarctinae, which in turn bear a greater resemblance to *Agriotherium* and *Indarctos*, and, amongst the latter, particularly the Florida specimen.

The relatively short and broad tremarctine snouts are, however, ursine-like in having the posterior palatine incisure well posterior of the M²'s (see Kurtén 1966, 1967). By contrast, in *A. africanum* the posterior ends of the M²'s are in line with this incisure. The situation in *Indarctos* is similar (e.g. *I. atticus* from Samos—Helbing 1932; Thenius 1959), except that in this instance the M²'s project slightly more posteriorly because, unlike these teeth in *Agriotherium*, they have a talon and are more anteroposteriorly elongated. *Ailuropoda* is virtually identical to *Indarctos* in this respect. The situation of the posterior palatine incisure relative to the M²'s sets *Agriotherium*, *Indarctos* and *Ailuropoda* apart from all other later ursids.

It is worth noting here that Davis (1964: 50) believed that the lengthened palate in *Ursus* relative to that in *Ailuropoda* 'is an illusion created by the large

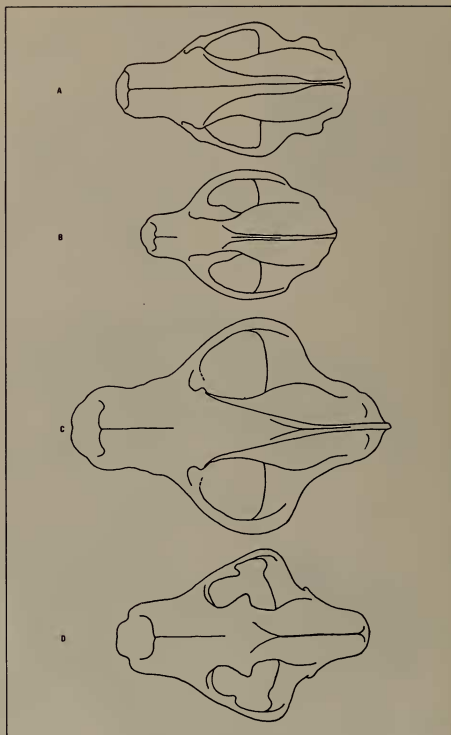


Fig. 3. Dorsal views of skulls. A. *Thalarcos*. B. *Ailuropoda*. C. The Langebaanweg *Agriotherium*. D. *Panthera leo*. A-B after Gregory (1936, figs 13-14).

teeth of the latter' and that relative 'to the anterior end of the braincase, the palate actually extends farther posteriorly in the panda.' This is true, but Davis makes no mention here of the great shortening of the posterior parts of the *Ailuropoda* skull, which undoubtedly has an effect on the position of the palate relative to the braincase.

The palate of L45062 is otherwise unremarkable, except that it lacks the minor posterior palatine foramen which is present in all other later ursids. In addition, it has a relatively small anterior median palatine foramen. In the latter respect it resembles *Indarctos* and *Ailuropoda*, and differs from the Ursinae and Tremarctinae. The minor posterior palatine foramen has apparently been incorporated with the major one, probably as a result of shortening of the palate. A vestige of the minor foramen is indicated on the posterior part of the major foramen by a shelf of bone projecting from the lateral wall of the latter. Earlier in the history of *Agriotherium* this shelf may well have extended to the medial walls of the major foramen, thus forming a separate minor foramen posteriorly.

The infraorbital foramen is situated above the posterior part of P⁴, as in *Indarctos*. This foramen is more posteriorly situated in Ursinae and some Tremarctinae, but is more anteriorly situated in *Ailuropoda*. It is relatively small compared with that in other Ursidae, and in those *A. africanum* specimens in which it is preserved (L2045, L45062, L41404) it is in the form of a single opening. In other ursids, such as the *A. sivalense* skull and some tremarctines, there may be more than one opening. The latter condition is probably of no great significance, since multiple infraorbital foramina have been observed in other carnivores (e.g. *Proteles cristatus*).

There is a marked concavity of the maxilla above the reduced anterior premolars, anteroventrally from the infraorbital foramen, which is caused by the expansion of the maxilla over the massive root of the canine and over the roots of the posterior cheek teeth. In anterior view the bulges over the canine roots completely obscure the infraorbital foramina. Amongst the Ursinae a similar tendency was observed in *Thalarchos*, although in this instance the infraorbital foramina were only partly obscured. Wolff's (1978: 2) description of the snout of the Florida *Indarctos* shows that it is essentially similar to *A. africanum*. The latter is distinct only in having features such as the bulge over the canine roots exaggerated, apparently because of the larger size of the Langebaanweg species. Wolff unfortunately provided few measurements of the Florida skull, and consequently most dimensions must be estimated from illustrations.

The nasal aperture of L45062 does not recede as markedly towards the nasals as it does in the Ursinae, and *A. africanum* resembles *Indarctos* and the Tremarctinae in this respect. This feature is evidently due to relative shortening of the snout.

Observations on the frontal region of L45062 are omitted, since there was severe fragmentation of this part of the skull and the restoration is not necessarily accurate. For example, the orbit appears smaller and the frontals more

inflated than in the skull of *A. sivalense*, in which this region is well preserved and therefore certainly accurate. It is nevertheless clear that the post-orbital processes of *A. africanum* are relatively less prominent than those of Ursinae, and the former is probably more like *Indarctos* (*I. atticus*) and *Ailuropoda* in this respect.

In his description of the zygomatic arches of *Ailuropoda*, Davis (1964: 47) stated that in dorsal view they 'form nearly a perfect circle, compared with the triangular outline in *Ursus* and other carnivores'. In *A. africanum*, which has exceedingly stout zygomata, their shape approaches that in *Ailuropoda*. The glenoid fossa and postglenoid process are also large, and in the postglenoid region a wide shelf of bone extends over the external auditory meatus, linking the zygomatic arch with the nuchal crest. The situation in *Indarctos* and *Ailuropoda* is similar, although in the latter the shelf of bone is much shorter, owing to the anteroposterior compression of the basicranial region in *Ailuropoda*. The shelf of bone is less well developed in the Ursinae.

Amongst fossil specimens the zygomata which most closely resemble those of L45062 belong to the Florida *Indarctos*, and once again Wolff's (1978: 2) description also applies to the Langebaanweg skull. The latter differs in apparently having zygomata of larger size, and in being more strongly arched and thus more *Ailuropoda*-like.

The sagittal crest of L45062 is extremely well developed, reaching a height of at least 50 mm, and, as in the Florida *Indarctos* (Wolff 1978: 2, 3), it has 'a very conspicuous cleft between the parietals'. It is, however, slightly deeper (up to 7 mm) and possibly longer (at least 70 mm) than that of the Florida skull. A similar cleft is found in the sagittal crest of *Ailuropoda* (Davis 1964).

According to Wolff (1978: 3), 'several large, rather irregularly sized and positioned nutrient foramina appear on either side of the parietals just above the temporal shelves near the posterior of the skull in several agriotheriine specimens', including the skull described by him. There are two such foramina in L41404, one on either side of the sagittal crest, immediately adjacent to it and close to its posterior limit. The same applies to L45062, but since this region of the skull is incomplete, it is possible that there were more than two such foramina.

The large size of the zygomata and enormous sagittal crest, together with various rugosities for muscle attachments similar to those of the Florida *Indarctos* (Wolff 1978), indicate that the masticatory musculature of *A. africanum* was exceptionally powerful, and in keeping with the massive canines and posterior cheek teeth of this species.

The basicranial regions of L45062, L41404, and L45137 are unfortunately poorly preserved and incomplete, although sufficient remains to show that they are ursid-like. Amongst the living Ursidae there are similarities to both Ursinae and *Ailuropoda*, while of described fossil specimens they closely resemble, and in several respects are indistinguishable from, the Samos *I. atticus* (Thenius 1949, 1959) and the Florida *Indarctos* (Wolff 1978).

As in *Ailuropoda* and *Indarctos*, the foramen rotundum and orbital fissure form a single opening in both L45062 and L41404. There is a well-developed horizontal division separating them a short distance posterior to the common opening as in the Florida *Indarctos*. In this respect *Ailuropoda* differs in that there is at most 'a paper-thin partition separating them' (Davis 1964: 49).

A. africanum is also like *Ailuropoda* and *Indarctos*, and different from most, if not all other Ursidae, in lacking an alisphenoid canal. In addition, *A. africanum*, *Indarctos*, and *Ailuropoda* are similar in that the medial edge of the glenoid fossa is closer to the foramen rotundum than is the case in the Ursinae, evidently because of the greater transverse length of this fossa in these three taxa.

The same applies in the case of the foramen ovale, which is preserved in L45062, L41404, and L45137. This foramen opens opposite the posterior wall of the glenoid fossa in these specimens, and they are similar to the Samos *I. atticus*, and probably also the Florida *Indarctos*, in this respect. In the Ursinae the foramen ovale is more posteriorly situated, while in *Ailuropoda* it is further forward.

The postglenoid foramen in *A. africanum* is situated between the external auditory meatus and the medial edge of the postglenoid process, but is closer to the latter than is the case with living ursids. Amongst the latter, *Ailuropoda* is the most distinct, since the postglenoid foramen is 'more laterally situated than in *Ursus*' (Davis 1964: 52). The situation in the Florida *Indarctos* and *I. atticus* is similar to that in *A. africanum*, although the specimen described by Thenius (1949) differs in having a double opening.

The external auditory meatus is incomplete in L45062, but it is evidently similar in position and orientation to that in the Florida *Indarctos*.

The anterior (squamosal) part of the mastoid process of L41404 is complete. It had not yet fused to the posterior (periotic) portion of this process, nor to the bone which caps this process. In size and orientation it is apparently similar to the mastoid process of the Florida *Indarctos*, and appears to have been more laterally directed than that of later ursids. Both the mastoid and paroccipital processes of L45062 are lost. The relative position of the bases of these processes differs from that in later ursids in that the base of the mastoid process is only slightly more laterally situated than that of the paroccipital process. The mastoid process of L45062 apparently differed from that of L41404 in being orientated ventrally.

Part of the lateral walls of the stylomastoid foramina, and the posterior margins of the posterior lacerate foramina, are preserved in L45062. Their positions relative to one another are as in the Ursinae and *Indarctos*. The same applies to the hypoglossal foramina and the anterior lacerate foramina.

Little of the bulla of L45062 remains. The posterior parts appear to have been more inflated than in *Ursus arctos*, and in this respect the bulla may have been more *Indarctos*-like. In overall size the bullae of *A. africanum* and a European *U. arctos* (ZM39056) were apparently similar, which is surprising in

view of the very much larger size of the *A. africanum* skull. In this respect *A. africanum* is also *Indarctos*-like. *Ailuropoda* is remarkable in that 'externally there is no indication of a bulla' (Davis 1964: 319, 320).

This is but one of the peculiarities of the *Ailuropoda* skull, which has been 'profoundly modified by the demands of mastication' (Davis 1964: 46). In less specialized ancestral forms the basicranial and other regions of the skull may well have resembled their counterparts in *Indarctos* and *Agriotherium* more closely than those in the Ursinae. The absence of the alisphenoid canal in *Indarctos*, *Agriotherium*, and *Ailuropoda* is probably the single most important basicranial character which distinguishes them from the Ursinae. This canal is present in the Canidae and all other Ursidae (Wolff 1978), including the Amphicyoninae (Ginsburg 1977; Hunt 1977) and, presumably, the Hemicyoninae.

The occipital region of *A. africanum* is known from L45062 (ventral parts) and L41404 (dorsal part and ventral part adjacent to, and including, the squamosal part of the mastoid process). In posterior view it is relatively narrow and steeply arched, rather like that of *U. arctos* and *Indarctos*. In L41404, which represents a young adult with some sutures unfused, there is an indication of a constriction above the mastoid process. In L45062, an older individual, the nuchal crest is strongly developed, and instead of passing ventrally directly on to the lateral side of the mastoid process, as in most living ursids, it is linked anteriorly with the shelf of bone which projects posteriorly from the zygomatic arch. The base of the mastoid process in L45062 is actually recessed beneath this shelf of bone. In most of the available ursine comparative specimens, the nuchal crest merges ventrally into a ridge of bone on the mastoid process, which is more laterally situated than the shelf extending posteriorly from the zygomatic arch. Only in *Thalarcos* does the arrangement approach that in *A. africanum*. It is not clear from illustrations of *I. atticus* (Thenius 1959) and the Florida *Indarctos* (Wolff 1978) which arrangement characterizes this genus.

The mandible is massive, its size being in keeping with that of the skull (Figs 4-5). It is similar in shape to that of *I. atticus* and *U. arctos*, and is distinguished principally by the presence of a premaseteric fossa. This fossa is deep in older individuals (e.g. L45062), but much less pronounced in immature adults (e.g. L45114) (Fig. 33). The only living bear with a premaseteric fossa is the South American spectacled bear, *Tremarctos ornatus*, while it is otherwise known amongst Ursidae in extinct Tremarctinae, Hemicyoninae and other species of *Agriotherium*. In tremarctines the masseteric and premaseteric fossae are separated by a prominent ridge of bone, and the latter fossa is deep, extensive and more or less circular in shape, with its limits clearly defined (e.g. see Kurtén 1966, plates 8-9). In hemicyonines the ridge separating the two fossae is not as prominent, the premaseteric fossa is less extensive in a vertical sense, but more elongated anteroposteriorly, with the anterior end gradually merging with the buccal surface of the mandible beneath M_1 (e.g. see Frick 1926, figs 2-3, 12).

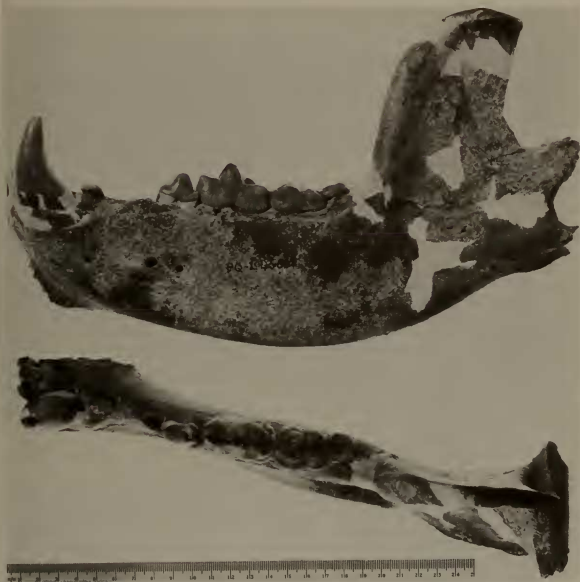


Fig. 4. Buccal and dorsal views of Langebaanweg *Agriotherium* hemimandible, L45062.

The premasseteric fossa in *Agriotherium* is closer to the hemicyonine type, and may even be virtually indistinguishable from it (e.g. the *A. insigne* specimen figured by Viret (1939, fig. 6)). There are, however, *Agriotherium* specimens in which this fossa does not extend as far anteriorly, terminating instead beneath M_2 (e.g. the *A. schneideri* specimen figured by Frick (1926, fig. 36)). There is at least one specimen assigned to *Agriotherium* in which this fossa is absent (i.e. the *A. palaeindicum* specimen, GSI-D8, discussed by Pilgrim (1932)). The latter is, however, one of the problematical intermediates between *Indarctos* and *Agriotherium*, which will be discussed in a later section of this report.

The premasseteric fossae in *A. africanum* specimens are generally similar



Fig. 5. Buccal and dorsal views of Langebaanweg *Agriotherium* hemimandible, L45114.

to that in the *A. schneideri* specimen mentioned above. In the four hemimandibles belonging to three individuals in which the entire premasseteric fossa is preserved, the anterior termination is beneath M_2 . These specimens apparently differ from hemicyonines and other *Agriotherium* in having a less distinct ridge of bone separating the masseteric and premasseteric fossae.

The mandible of *A. africanum* is otherwise distinguished only by the presence of a distinct 'chin' in the symphyseal region, which contrasts with the receding jaw-line in other ursids. The 'chin' is formed by an anteroventral expansion of the symphysis, which enlarges the area of the symphysis and presumably strengthened the connection between the two halves of the mandible.

With the exception of the nondescript and relatively unimportant I^1 , P^1 , P_2^2 and P_3 , all the teeth of *A. africanum* are known from at least one complete specimen still in position in a jaw. An incomplete I^1 is represented in L45062, while P^1 and P^2 are tentatively identified on the basis of isolated specimens. Only P_2 and P_3 have not been identified, although they could be represented amongst the six unidentified anterior premolars available. The best represented of the teeth are the larger posterior cheek teeth ($P_4^4-M_2^2$), which are, fortunately, the most informative in the dentition of *Agriotherium* (Figs 2, 6-7; Tables 2-3). These teeth are represented by between six and ten specimens belonging to between four and seven individuals.

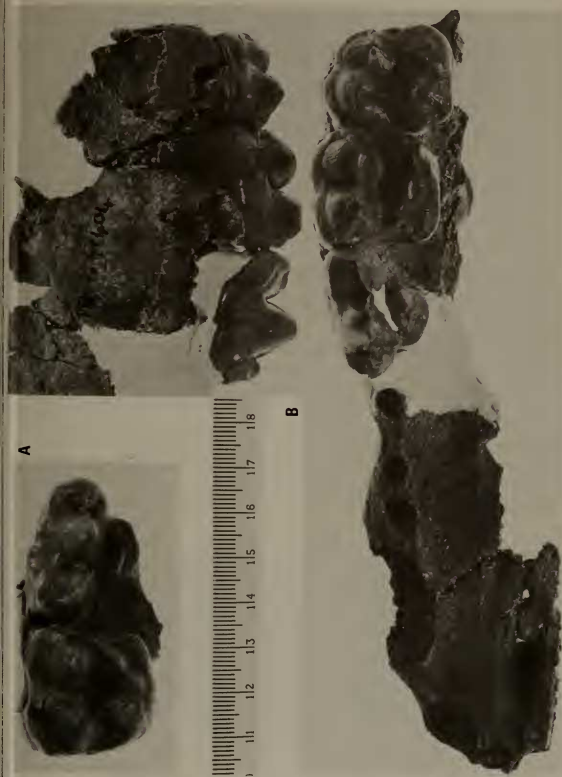


Fig. 6. A. Ventral view of Langebaanweg *Agriotherium* maxillary fragment, L55012. B. Buccal and ventral views of snout fragment, L41404.



Fig. 7. Ventral view of Langebaanweg *Agriotherium* maxillary fragment, L45137.

Apart from their large size, the incisors of *A. africanum* are unremarkable and are little different from those of living Ursinae. Dimensions of some incisors were given elsewhere (Hendey 1977, tables 2, 5). The I^2 is distinct in having two lingual cusps projecting from the V-shaped cingulum posterior to the principal (spatulate) cusp. The lateral accessory cusp is the smaller and the more anteriorly situated, being little more than a small projection from the cingulum. The other accessory cusp is much larger, covering much of the lower part of the lingual surface, although it is still much smaller than the principal cusp (Fig. 8). In older individuals (e.g. L45062) the three cusps develop horizontal wear facets in a single plane. The I^1 is similar to I^2 , but smaller, while the I^3 , which is the largest of the incisors, is morphologically similar to its counterpart in Ursinae.

The lower incisors are similar to those of *Ursus arctos* and other ursines, and are distinguished only by their larger size.



Fig. 8. Medial, posterior and lateral views of Langebaanweg *Agriotherium* I^2 , unnumbered Dump 8 specimen.

TABLE 2
Dimensions of Langebaanweg *Agriotherium* upper teeth.

NUMBER	HORIZON	L/R	C		P ³		P ⁴		M ¹		M ²	
			l	b	l	b	l	b	l	ab	l	ab
L2045	. . bed 3aS	L	—	—	—	—	c. 32,8	25,5	—	—	—	—
L45062	. . bed 3aN	L	27,0	c. 21,0	9,5	7,5	32,6	24,3	28,1	30,0	26,4	29,9
		R	27,8	21,2	9,7	7,6	31,9	c. 24,5	28,5	29,5	26,5	30,2
L45137	. . bed 3aN	L	29,2	20,6	—	—	31,6	22,0	30,3	29,1	c. 29,3	31,5
		R	c. 29,2	c. 21,6	—	—	31,2	22,7	29,8	28,9	29,5	31,4
L41404	. . bed 3aN	L	—	—	—	—	32,5	24,2	28,5	30,9	26,5	31,0
L55012	. . bed 3aN	L	—	—	—	—	33,0	24,4	—	—	—	—
		R	—	—	—	—	33,0	25,0	29,2	28,6	—	—
L46074	. . bed 3aN	R	—	—	—	—	33,3	24,1	—	—	—	—
L50008	. . bed 3aN	R	—	—	—	—	35,8	c. 25,0	—	—	—	—
L48564	. . bed 3aN	L	—	—	—	—	—	—	—	—	25,6	30,5
L48577	. . bed 3aN	R	—	—	—	—	—	—	—	—	25,4	30,2
L47242	. . bed 3aN	R	—	—	—	—	—	—	—	—	25,8	25,9
L47698	. . bed 3aN	L	—	—	—	—	—	—	—	—	31,1	30,1
Means	28,3	21,1	—	—	32,8	24,2	29,1	29,5	27,5	30,1
Ranges	27,0– 29,2	20,6– 21,6	—	—	31,2– 35,8	22,0– 25,5	28,1– 30,3	28,6– 30,9	25,4– 31,1	25,9– 31,5
n	4	4	—	—	10	10	6	6	9	9

L = Left ; R = Right

TABLE 3

Dimensions of Langebaanweg *Agriotherium* lower teeth.

NUMBER	HORIZON	L/R	\bar{C}		P_1		P_2		M_1			M_2		M_3	
			l	b	l	b	l	b	l	ab	pb	l	b	l	b
L12561 .	bed 3aS	R	—	—	—	—	—	—	—	—	—	—	—	16,5	16,7
L45062 .	bed 3aN	L	29,8	19,8	12,8	8,1	21,8	14,2	39,7	20,3	23,0	29,3	24,0	16,2	16,6
		R	c. 29,0	—	12,8	8,3	c. 22,4	14,0	39,7	19,7	22,3	28,6	c. 23,6	17,1	17,0
L46563 .	bed 3aN	L	—	—	—	—	—	—	—	—	—	33,5	24,3	—	—
L45114 .		R	33,8	21,7	—	—	25,4	15,5	43,1	20,7	22,8	32,6	23,5	—	—
L50003 .	bed 3aN	L	—	—	—	—	24,5	15,5	—	—	—	30,4	24,1	—	—
L50004 .	bed 3aN	L	—	—	—	—	24,0	16,8	43,4	22,1	24,8	32,3	26,0	—	—
L50445 .	bed 3aN	L	—	—	—	—	23,5	15,0	—	—	—	—	—	—	—
L50446 .	bed 3aN	R	—	—	—	—	—	—	44,0	19,8	23,4	—	—	—	—
L50005 .	bed 3aN	R	—	—	—	—	—	—	43,9	20,2	22,9	—	—	—	—
L50006 .	bed 3aN	L	—	—	—	—	—	—	37,8	18,5	21,1	—	—	—	—
L50007 .	bed 3aN	R	—	—	—	—	—	—	—	—	—	28,8	21,9	—	—
L50981 .	bed 3aN	L	—	—	—	—	—	—	—	—	—	—	—	19,8	19,0
Means	30,9	20,8	—	—	23,6	15,2	41,7	20,2	22,9	30,8	23,9	17,4	17,3
Ranges	c. 29,0– 33,8	19,8– 21,7	—	—	21,8– 25,4	14,0– 16,8	37,8– 44,0	18,5– 22,1	21,1– 24,8	28,6– 33,5	21,9– 26,0	16,2– 19,8	16,6– 19,0
n	3	2	—	—	6	6	7	7	7	7	7	4	4

L = Left ; R = Right

The canines are similarly remarkable only for their large size. Otherwise they differ from the canines of Ursinae only in being less elongated anteroposteriorly.

All the known anterior premolars (P_1^1 to P_3^3) are small, low-crowned and single-rooted teeth. The P_1 is slightly elongated anteroposteriorly, and the crown is divided longitudinally by a crest in the enamel. This is evidently the remnants of the anterior and posterior keels which have merged into a single feature as a result of reduction of the principal cusp, and its disappearance as an identifiable element in this tooth. The enamel on the buccal side of the crest is smooth, while that on the lingual side is slightly rugose. The P^3 is similar, but is more circular in outline, while the crest is convex buccally, with vestiges of the principal cusp still evident. The tentatively identified P^1 (L55017A) fits the P^1 alveolus of L45062 well and may even belong to this specimen. It is similar to P_1 , but is slightly broader posteriorly, and with vestiges of the principal cusp still evident.

The P_4 of *A. africanum* is much larger than the anterior premolars, and in relative size and morphology it is not unlike its counterpart in the Ursinae. It is a stout, double-rooted tooth, with a prominent principal cusp, and in lateral view the anterior and posterior halves are almost mirror images of one another. The tooth is broader posteriorly due to the presence of a postero-lingual bulge in the cingular region. The anterior and posterior keels of the principal cusp are well defined but rather blunt, and terminate ventrally on cuspless horizontal shelves. The posterior shelf is fringed by a well-developed cingulum. Much of the P_4 enamel is finely rugose, which is also the case in other posterior cheek teeth of *A. africanum*. The apex of the principal cusp develops a horizontal wear facet, which merges with an inclined facet on the posterior keel.

The P^4 of *A. africanum* (Fig. 9) is an important tooth, since it was largely on its characteristics that the species was identified (Hendey 1972). The P^4 of the holotype (L2045) has been exhaustively described (Hendey 1972; Wolff *et al.* 1973), while examples from the bed 3aN sample have been briefly discussed (Hendey 1977). The P^4 of L2045 is unlike that of any previously described *Agriotherium* because of the presence of a large accessory cusp antero-internally, that is, the anterior end of the protocone lobe. It is now evident that this feature also distinguishes it from the P^4 's of the bed 3aN sample, in which this cusp may be present but small (e.g. L45137), or very small (e.g. L45062), although it may also be absent (e.g. L41404). The P^4 of the *A. africanum* holotype is thus atypical of the species sample as a whole. It is, however, not necessarily an abnormal specimen, but may well be a typical example from a population which predates, and is therefore more primitive than that represented in bed 3aN.

The bed 3aN P^4 sample, which is comprised of nine specimens belonging to six individuals, includes only one in which the antero-internal cusp is absent (i.e. L41404). Consequently, this cusp can still be regarded as a characteristic of the species. A similar situation does, however, exist in respect of the *A. insigne*



Fig. 9. Buccal, occlusal and lingual views of Langebaanweg *Agriotherium* P⁴'s.
A. L46074, from bed 3aN. B. L2045, from bed 3aS.

from Montpellier in France. A specimen described by Gervais (1859) apparently lacks an antero-internal cusp, but an undescribed specimen from the same locality (NMB-MP549) has a large antero-internal cusp on its P^4 . For this, and other reasons, *A. africanum* should perhaps be regarded as a junior synonym of *A. insigne*, a matter which will be pursued in a later section of this report.

There is apparently one feature of P^4 in which *A. africanum* may be unique. In L2045 there is a small wear facet situated between the antero-internal cusp and the apex of the protocone, which was interpreted as the vestiges of another accessory cusp on the protocone lobe by Hendey (1972). Wolff *et al.* (1973) dismissed this interpretation, and regarded this feature simply as a wear facet caused by occlusion with M_1 . It is undoubtedly such occlusion which caused the wear facet, but Wolff and his co-authors overlooked the fact that it is impossible to get dentine exposed at the same level as enamel unless there had previously been a small cusp in this position. The difference of opinion is conclusively resolved by the fact that the bed 3aN sample includes unworn examples of this accessory 'intermediate' cusp. It has already been recorded elsewhere (Hendey 1977: 114) that the P^4 of L41404, although lacking an antero-internal cusp, does have 'a small, more posteriorly situated cusp which apparently corresponds to the "intermediate cusp" of the holotype'. Another specimen is now known (L46074) in which both an antero-internal cusp and an 'intermediate cusp' are present and unworn. As with the antero-internal cusp, the 'intermediate cusp' of L2045 must have been more prominent than that of any bed 3aN specimen.

The buccal cusps of the *A. africanum* P^4 are unremarkable. All ten specimens have prominent parastyles, which is characteristic of the genus and of some advanced *Indarctos* specimens (see p. 81). The P^4 has three roots, two beneath the buccal cusps and one beneath the lingual ones. The M^1 and M^2 of *A. africanum* are similar in this respect, although the lingual root is larger in these teeth.

The wear facets on P^4 were discussed by Hendey (1972) and Wolff *et al.* (1973), and the only additional observation possible is that the parastyle develops a crescentic facet which is inclined anterolingually.

The seven M_1 's belonging to four *A. africanum* individuals are, in general, similar to those of previously described *Agriotherium* (Fig. 10A). The trigonid makes up the bulk of the tooth, with the protoconid being particularly large and prominent. Although the shearing facets normally found in carnivore lower carnassials are evident on the buccal surfaces of the paraconid and protoconid, the apices of these cusps also develop horizontal facets. In addition, the single anterior, and two divergent posterior keels of the protoconid may be obliterated by inclined facets. Cingula are developed on both sides of the paraconid, with that on the lingual side being more pronounced. There are usually only two talonid cusps clearly developed, a prominent, rather bulbous one on the lingual side, and a low, ridge-like one on the buccal side. The latter develops a horizontal wear facet, while the large lingual cusp develops a posterobuccally



Fig. 10. Lingual, occlusal and buccal views of Langebaanweg *Agriotherium* M_1 's. A. L50004, a male specimen of typical morphology. B. L50006, a female specimen with vestigial ?metaconid.

inclined facet. There is a ridge of enamel posterior to this cusp which may take the form of a low cusp, as in L50004.

There are two M_1 's in the assemblage which deviate from the basic cusp pattern described above. An isolated specimen, L50006, which is the smallest of the M_1 's, and which evidently belonged to a female, has a small additional cusp situated between the protoconid and the large lingual talonid cusp (Fig. 10B). This specimen is also unusual in having only a lingual posterior keel on the protoconid, the buccal one, which is usually less pronounced, being absent. In addition, the ridge anterior to the buccal talonid cusp is directed towards the additional cusp, rather than directly anteriorly as is usually the case. The second unusual M_1 is L50446, which is distinct in having two small cusps situated posterior to the large lingual talonid cusp. The possible significance of these specimens will be discussed later (see pp. 83, 84).

Both M_1 and M_2 have two roots, a larger one supporting the trigonid and the other supporting the talonid.

The M^1 of *Agriotherium* has the basic four-cusped pattern typical of all later ursids, and this tooth of *A. africanum* is little or no different from its counterparts in previously described *Agriotherium*. The paracone and metacone are prominent conical cusps of similar size, which develop horizontal wear facets on their apices, and inclined facets posterolingually. The protocone is a ridge-like cusp directed anterobuccally at a slight angle to the anteroposterior axis of the tooth. The hypocone is conical and less voluminous than the protocone. The two lingual cusps are lower crowned than the buccal ones. There are lingual and buccal cingula which are distinct largely because the enamel is smooth, whereas that elsewhere tends to be rugose. The cingular region bulges anterolingually, and this results in the length of the tooth measured over the lingual cusps being close to the buccal (maximum) length. In addition, the breadth measured over the two anterior cusps is comparable to the posterior breadth measurement, and to the two length measurements. In other words, the M^1 of *A. africanum* is more or less square in outline. *Agriotherium* is unique amongst later ursids in this respect. In the Ursinae, Tremarctinae, *Indarctos* and *Ursavus* the M^1 's are rectangular with lengths exceeding breadths, while in *Ailuropoda* the situation is reversed and the M^1 is broader than it is long.

The M_2 of *A. africanum* also has a basic four-cusped pattern, but in this instance the two largest cusps (paraconid and protoconid) are situated anteriorly, rather than buccally as in M^1 (Fig. 11A). There are, however, three teeth belonging to at least two individuals which deviate from this pattern. They are L45115 and L46563 (Figs. 5, 11B) which probably belong to one individual, and L50007, which belongs to a smaller individual, probably a female. In these specimens the anterolingual cusp is reduced or absent. Reduction is evident in L50007 where the anterolingual cusp is situated closer to the anterobuccal cusp, with its anterior and posterior keels directed accordingly. This gives the impression that it is merging with the anterobuccal cusp, rather than simply reducing in its usual position. In L45114/L46563 the anterolingual

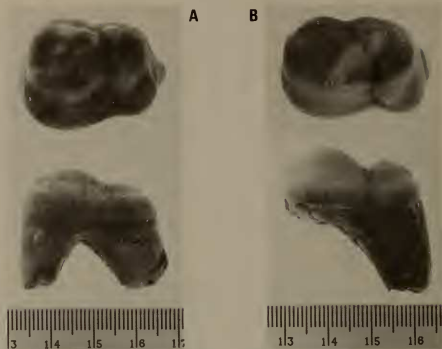


Fig. 11. Occlusal and buccal views of Langebaanweg *Agriotherium* M_2 's. A. L50004, a specimen of typical morphology. B. L46563, a specimen lacking the anterolingual cusp.

cusp is absent, and its posterior keel is linked to the apex of the anterobuccal cusp. Only vestiges of the anterior keel remain. These three teeth are also distinct in being relatively narrower than others in the M_2 sample. The M_2 cusps develop horizontal wear facets, while there are also inclined facets antero-buccally and on the buccal surface of the posterobuccal cusp.

The M^2 of *A. africanum*, like the P^4 , is an important tooth, and it is fortunately well represented (Fig. 12). It is essentially similar to M^1 in its basic cusp

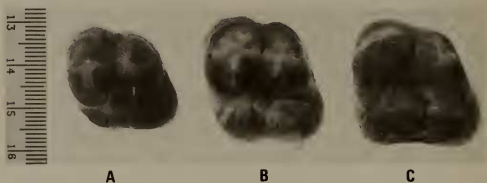


Fig. 12. Occlusal views of Langebaanweg *Agriotherium* M^2 's. A. L47242 (reversed). B. L48564. C. L47698.

morphology. The paracone and metacone are the most prominent of the four cusps, although in this instance the metacone is a little smaller than the paracone. The protocone is ridge-like, while the hypocone is more conical, although it tends to be less distinctly developed than the other cusps. There is an expansion of the lingual cingulum adjacent to the protocone, and sometimes also in the posterolingual part of the tooth. The latter expansion is significant since it represents the vestiges of the talon which was present in ancestors of *Agriotherium* (see page 87). As with the other molars, the cusps develop horizontal wear facets, while there are also inclined facets developed anterolingually on the paracone and metacone.

The M_3 of *A. africanum* is a relatively simple, single-rooted tooth, which tends to be circular in occlusal view, with no distinct cusps developed (Fig. 13).

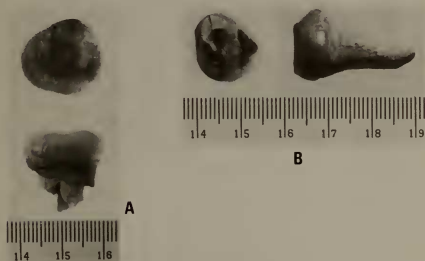


Fig. 13. A. Occlusal and lingual views of Langebaanweg *Agriotherium* M_3 , L50981.
B. Occlusal and posterior views of M_3 , L12561.

The occlusal surface is in the form of a shallow basin surrounded by a low ridge of enamel. This ridge develops a horizontal wear facet, and the entire occlusal surface would presumably be worn flat in older individuals. There is also an inclined wear facet anterobuccally. This region of the tooth tends to be slightly expanded, which emphasizes a posterior tapering which is best seen in the specimen L50981.

More detailed comparisons between the teeth of *A. africanum* and other taxa will be made in a later section of this report.

THE POSTCRANIAL SKELETON

The present study of *A. africanum* postcranial bones has been superficial, largely because adequate modern comparative material was not available and



Fig. 14. Lateral and ventral views of Langebaanweg *Agriotherium* scapula, L50858. Arrow indicates postscapular fossa.

because of the lack of direct access to relevant fossil material. Little has hitherto been published on the postcranial skeleton of *Agriotherium* and other late Tertiary ursids, and although meaningful interpretation of the evolutionary and functional significance of *A. africanum* bones is no doubt possible, the following account of them is essentially descriptive. In this account references are made to bones of a male European *Ursus arctos* (ZM39056), a male Asian *Euarctos* (ZM38805) and a female *Helarctos* (ZM36289), all of which are zoo specimens. Reference is also made to the limb bones of *Ailuropoda* as described by Davis (1964).

In general, the bones of *A. africanum* are larger and more stoutly proportioned than those of the *U. arctos* comparative specimen, but they are essentially similar morphologically.

The available vertebrae of *A. africanum* are all incomplete, and most are very fragmentary. Except for their larger size, they are similar to those of the available comparative specimens and *Ailuropoda*. No ribs definitely identified with *A. africanum* are known.

The only identified *A. africanum* scapulae, L50857/8, may belong to one individual, although L50858 differs in showing indications of mild osteoarthritis (Fig. 14). Both specimens lack most of the blades. The glenoid fossa is anteroposteriorly elongated and tapers anteriorly, much like those in the ursine comparative specimens and the *Ailuropoda* specimen illustrated by Davis (1964, fig. 46). The preserved parts of the blades of *A. africanum* scapulae are also similar to those of ursines and *Ailuropoda*, except for one marked difference which may be of great functional significance.

Davis (1964: 91) has recorded that there are differences in the nature of the postscapular fossae in *Ailuropoda* and *U. arctos*, and, judging from the available comparative specimens, there is appreciable variation of this fossa in Ursinae. It is only the lower parts of this fossa which can be observed in L50857/8, and these specimens are distinct in having the inferior scapula spine terminating on the lateral surface of the blade 50 to 60 mm above the glenoid fossa, instead of terminating posteriorly at the glenoid fossa. Consequently, the postscapular fossa in *A. africanum* is confined to the lateral surface of the scapula, whereas the lower part of this fossa is on the medial surface in *Ailuropoda*, *U. arctos* and *Helarctos*, and posteromedially in Asian *Euarctos*.

According to Davis (1964: 91, 173) the postscapular fossa 'lodges the subscapularis minor muscle' which is the main 'medial rotator of the arm'. The functional significance of its distinct orientation in *A. africanum* is not known.

No complete humerii of *A. africanum* are preserved, the best available specimen being L45063, in which the proximal end is detached and slightly crushed, and part of the proximal part of the shaft is lost (Fig. 15, Table 4). The humerus is otherwise known from several fragmentary specimens, mainly distal ends. All the important features of the humerus, except overall length, can be observed. It is one of the many *A. africanum* bones in which available speci-



Fig. 15. Posterior, lateral and anterior views of Langebaanweg *Agriotherium* humerus, L45063.

mens exhibit appreciable size variation, larger specimens presumably belonging to males and smaller ones to females. The latter include L45063.

In its basic morphology the humerus of *A. africanum* is similar to those of Ursinae. Proximally it is similar to corresponding parts of ursine humeri in all observable respects, but distally there are some differences, although like the Ursinae, and unlike Tremarctinae and *Ailuropoda*, it lacks the entepicondylar foramen. However, vestiges of the bar of bone enclosing this foramen, in the

TABLE 4
Dimensions of Langebaanweg *Agriotherium* humerii.

	L40040	L45063
Max. ant.-post. diam., distal end . . .	91,7	67,0
Max. transv. diam., distal end . . .	121,5	98,5
Max. transv. diam., distal articulation .	92,7	76,4

form of a rugosity at its proximal termination, are more obvious in *A. africanum* than Ursinae.

The olecranon fossa is deep and relatively narrower than its counterparts in available ursine humerii, although it is closer to the Ursinae than *Ailuropoda* in this respect (see Davis 1964: 95, fig. 49). There is a relatively greater antero-posterior development of the *A. africanum* humerus distally, although once again it is closer to Ursinae than *Ailuropoda*. The medial epicondyle is much less prominent than in ursines, although the lateral epicondyle is similarly developed.

The lateral epicondylar ridge is more constricted above the lateral epicondyle than in ursines. This ridge has a relatively greater length than those of *U. arctos* and *Helarctos*, but that of Asian *Euarctos* is comparable in this respect. This is a reflection of the relatively greater elongation of the humerii in *A. africanum* and *Euarctos*.

The proximal termination of the lateral epicondylar ridge is more or less opposite the point of convergence of the deltoid and pectoral ridges (the deltoid tuberosity), as in ursines. The pectoral ridge is much like that of ursines, but the deltoid ridge is more prominently developed, and proximally it is more anteriorly situated. Consequently, the area between these two ridges faces anteriorly over a greater distance than in the ursines. This is the area of insertion of the cephalohumeral muscle, which is the chief extensor of the foreleg (Davis 1964: 95, 167). The functional significance of the more anterior insertion, and apparently greater development of this muscle, is not known.

Some of the characteristics of the ulna of *A. africanum* have already been discussed elsewhere (Wolff *et al.* 1973), but more and better specimens are now available (Fig. 16, Table 5). Once again the most complete specimen is L45063, which belongs to a smaller individual than the previously described specimen (L2154). Apart from the size difference, these two specimens are similar in all observable respects. The *A. africanum* ulna resembles those of available ursine specimens, and other ursids, including the *Indarctos atticus* specimen from Samos described by Pilgrim (1931). The proportions of L45063 are similar to those of the *U. arctos* comparative specimen.

In lateral view the *A. africanum* olecranon does not project as markedly as in ursines, and its medial tapering is usually less pronounced. The olecranon is, however, very broad transversely. The area for insertion of the triceps and flexor carpi ulnaris muscles is therefore large, although that for the insertion of the latter is less knob-like. In the Ursinae and *Ailuropoda* the area for insertion of the most proximal part of the anconeus muscle is prominently developed (see



Fig. 16. A. Medial view of Langebaanweg *Agriotherium* ulna, L46076. B. Anterior and lateral views of ulna, L45063.

TABLE 5
Dimensions of Langebaanweg *Agriotherium* ulnae.

	L50763	L50805	L50808	L40044	L12383	L46076	L45062(R)	L2154	L45063
Overall length	—	—	—	—	—	—	—	—	416,0
Transv. diam. of anconeal process	28,0	—	—	—	27,6	26,5	25,8	—	22,6
Transv. diam. of coronoid process at radial notch	47,0	—	—	—	41,6	42,1	40,7	38,4	38,5
Diam. of semilunar notch	45,6	—	—	—	41,5	44,0	40,7	—	39,7
Ant.-post. diam. at anconeal process	93,8	—	—	—	—	86,5	84,5	—	74,5
Ant.-post. diam. at semilunar notch	58,0	—	—	—	—	56,0	60,6	56,0	46,0
Ant.-post. diam at coronoid process	—	—	—	—	—	87,5	94,2	—	68,8
Long diam. of styloid process	41,7	—	41,5	38,8	—	—	—	—	32,0
Short diam. of styloid process	22,6	22,6	22,2	22,2	—	—	—	—	20,0

(R) = Right

Davis 1964: fig. 50), but is less so in *A. africanum*, especially female specimens such as L45063. Once again, the functional significance of these differences is not known.

The semilunar notch differs from those of ursines and *Ailuropoda* in some respects. In lateral view it is almost perfectly semicircular, with the inner borders of the notch not divergent at their extremities as in ursines, and not showing the beginnings of convergence as in *Ailuropoda* (see Davis 1964, figs 50–51). In anterior view the dorsal part is nearly parallel-sided, rather than sharply tapering as in ursines. The anconeal process of *A. africanum* is therefore relatively broad. This, and the relatively narrow olecranon fossa of the humerus, are probably directly related features. When the humerus and ulna of *A. africanum* are articulated and fully extended the olecranon fossa is nearly completely filled by the anconeal process, and little lateral movement of the ulna is possible. In the ursines only about half the olecranon fossa is filled and appreciable lateral movement is possible. Much the same evidently applies in the case of *Ailuropoda*, which has an even wider olecranon fossa than ursines, while Davis (1964: 96) noted that there was no protection against lateral shifting of the elbow joint. The significance of these contrasting situations is not known.

The shaft of the *A. africanum* ulna is very stout, and although the areas for attachment of the brachialis tendon and interosseous ligament vary both in size and form, they are very pronounced features.

Distally the radial articular facet is relatively, and sometimes absolutely, smaller than its counterpart in ursines. Medially between this facet and the styloid process is a deep and almost circular depression, which is directly in line with the prominent ridge on the shaft separating the areas of insertion of the pronator quadratus and the distal part of the flexor digitorum profundus 5 muscles. This depression is absent in available ursine specimens, and apparently also in *Ailuropoda* (Davis 1964, fig. 50). Its significance is not known.

The radius of *A. africanum* is represented by several proximal and distal fragments, but only one that is complete (L40044), while another has been restored (L45063) (Fig. 17, Table 6). The latter belongs to a female and L40044 to a male. These two specimens differ only in size. They are typically ursid in their characteristics, the proximal end being particularly distinctive, and L40044 is very similar in its proportions to the *I. atticus* specimen described by Pilgrim (1931). The latter specimen is, however, distinct in having a broad groove on the anterior surface towards the distal end. Pilgrim (1931: 27) thought this noteworthy since 'a similar structure exists in a corresponding position in the radius referred by Falconer to *Agriotherium* . . . *sivalense*'. According to Pilgrim it is also present in *Amphicyon*, although it is evidently not characteristic of all amphicyonines (see Ginsburg 1977, fig. 25). Since the radius of *A. africanum* is otherwise unremarkable, it is not described in detail.

With one exception, all the carpal bones characteristically present in Ursidae are represented by at least one, and as many as nine, complete specimens (Fig. 18, Table 7). The exception is the radial sesamoid, which was evi-



Fig. 17. A-B. Medial views of Langebaanweg *Agriotherium* radii. A. L45063. B. L40044. C. Proximal view of L40044.



Fig. 18. Carpal bones of Langebaanweg *Agriotherium*. A-G. L45063. H. L46134. I. L50767 (reversed). A. Proximal and dorsal views of scapholunar. B. Medial view of cuneiform. C. Medial and dorsal views of unciform. D. Anterior view of pisiform. E. Proximal, dorsal and lateral views of magnum. F. Proximal view of trapezoid. G. Lateral view of trapezium. H.-I. Specimens illustrating size range of scapholunars.

TABLE 6
Dimensions of Langebaanweg *Agriotherium* radii.

	L50806	L48747	L45062	L40044	L47699	L33826	L45063	L50816	L40003
Overall length	—	—	—	404,0	—	—	345,0	—	—
Max. ant.-post. diam., proximal end	44,1	43,8	—	41,6	c. 38,5	37,8	36,5	34,7	33,7
Max. transv. diam., proximal end	56,4	56,2	52,8	50,7	c. 49,0	50,3	45,4	47,4	—
Max. ant.-post. diam., distal end	—	—	—	49,0	—	—	c. 42,5	—	—
Max. transv. diam., distal end	—	—	—	70,5	—	—	63,7	—	—

TABLE 7
Dimensions of Langebaanweg *Agriotherium* carpals.

	SCAPHOLUNARS					PISIFORMS			
	L46134	L50635	L45062	L45063	L41702	L48021	L50767	L46134	L45063
Max. ant.-post. diam.	67,0	62,8	60,2	58,0	55,7	48,3	45,6	53,8	52,2
Max. ant.-post. diam. of radial facet	38,6	38,6	38,1	34,0	33,8	30,9	29,1	39,0	36,5
Max. transv. diam.	63,9	60,0	61,5	53,1	55,0	49,1	44,5	26,7	22,9
Max. dorsoventral diam.	38,0	—	39,2	35,2	33,8	c. 28,5	26,5	42,7	38,0
								28,7	28,4
								30,0	30,0
								30,0	23,8
	CUNEIFORMS					MAGNUMS			
	L50795	L45062	L45063	L50786	L50794	L33160	L50457	L47074	L45062
Max. ant.-post. diam.	48,0	44,3	38,7	—	43,3	41,6	38,9	38,7	38,5
Max. transv. diam.	42,0	36,7	32,5	31,5	24,3	22,0	20,3	21,5	20,8
Max. dorsoventral diam.	—	—	—	—	36,5	34,1	33,0	36,0	33,1
								28,8	28,8
								34,5	34,5
								30,4	30,4
								33,5	33,5
								33,6	30,1
								37,6	33,9
								34,9	34,9
	UNCIFORMS					L45063			
	L50772	L45062	L45063	L50774	L45063	L45062	L45063	L50772	L45063
Max. ant.-post. diam.	39,1	38,0	33,5	30,4	39,1	38,0	33,5	30,4	33,5
Max. transv. diam.	36,2	33,6	30,1	30,6	36,2	33,6	30,1	30,6	33,6
Max. dorsoventral diam.	42,8	37,6	33,9	34,9	42,8	37,6	33,9	34,9	33,9

dently absent in *A. africanum*, since the scapholunar lacks the radial sesamoid facet. In this respect *A. africanum* is very different from *Ailuropoda*, in which the radial sesamoid is better developed than in any other arctoid carnivore (Davis 1964: 99, 100). A small radial sesamoid is apparently usually, or always, present in Ursinae, and is larger in Tremarctinae. Otherwise the carpals of *A. africanum* are essentially similar to their counterparts in Ursinae.

The largest carpal, the scapholunar, is also the best represented. As with other *A. africanum* bones, the scapholunars exhibit appreciable size differences, the smallest (L50767) being only about two-thirds the size of the largest (L46134) (Fig. 18H-I). This is a slightly greater size difference than that observed in the scapholunars of North American *Tremarctos floridanus*, an ursid of similar overall size (Kurtén 1966, table 19), although in both instances sample sizes are small. There are no significant morphological differences between the smallest and largest scapholunars, and they differ in only minor respects from those of ursines. In the latter the cuneiform facet tends to be clearly distinct from the unciform facet, but in *A. africanum* they merge and are distinguishable only because the cuneiform facet is flattened and the unciform facet is concave. In some specimens (e.g. L48021) the proximal (radial) articular surface is in contact anteriorly with the articular facet of the trapezium, and in this respect *A. africanum* is similar to *Ailuropoda* (see Davis 1964: 99). The proximal articular surface of the *A. africanum* scapholunar is also *Ailuropoda*-like, and different from Ursinae, in lacking the lateral depression which receives 'the saddle on the distal end of the radius' (Davis 1964: 99).

The cuneiform of *A. africanum* is morphologically similar to that of *U. arctos*, except that the scapholunar facet is more elongated. In addition, this bone is relatively more flattened than that of *U. arctos*.

Such minor differences in morphology and proportions also distinguish other *A. africanum* carpals from their *U. arctos* counterparts. For example, in the *A. africanum* unciform, the magnum and scapholunar facets are not confluent as in *U. arctos*, while the pisiform is a considerably stouter bone. At least some of the distinctive features in *A. africanum* carpals may be due to the large size of the species, but their possible significance in other respects was not investigated.

Of the metacarpals of *A. africanum* only the second is not represented by a complete specimen, although there is one which lacks only the distal end (L33160). All the metacarpals are similar to their counterparts in ursines in terms of morphology, but are relatively more massive (Fig. 19, Table 8). In spite of this, they are not necessarily much longer than those of the available *U. arctos* specimen. One of the complete metacarpals I (L45448) is in fact similar in length to that of the *U. arctos* comparative specimen, although it has a much stouter proximal end and shaft. The *A. africanum* metacarpals appear to be readily distinguishable from those of *Ailuropoda*, which are 'short and stout, relatively considerably shorter than in [other bears] of comparable size' (Davis 1964: 100).



Fig. 19. Proximal, anterior and lateral or medial views of Langebaanweg *Agriotherium* metacarpals. A. I, L50775. B. III, L25862. C. IV, L33828. D. V, L45063.

TABLE 8
Dimensions of Langebaanweg *Agriotherium* metacarpals.

	I				II		III				
	L50775	L45063	L55029	L45448	L33160	L33160	L50810	L25862	L20998	L45062	L50788
Overall length	81,2	—	81,2	79,9	—	—	—	121,9	113,6	—	117,5
Max. ant.-post. diam., prox. end	25,3	23,0	22,7	—	24,8	—	37,8	—	36,2	32,6	31,8
Max. transv. diam., prox. end	25,7	22,2	23,6	—	34,6	—	23,5	—	22,0	20,4	20,7
Max. ant.-post. diam., dist. articulation	17,4	—	17,3	17,2	—	—	—	24,8	24,5	—	23,5
Max. transv. diam., dist. articulation	18,7	—	17,9	17,3	—	—	—	23,0	24,8	—	22,0
	IV				L45063	L33160	V				
	L33160	L48432	L33828	L41575	L45063	L33160	L33160	L45063	L50810	L25862	L20998
Overall length	—	126,1	120,4	117,7	—	—	—	106,2	—	—	—
Max. ant.-post. diam., prox. end	37,5	36,3	34,3	—	32,3	—	37,0	29,9	—	—	—
Max. transv. diam., prox. end	26,0	26,3	23,1	22,4	20,4	—	33,5	25,7	—	—	—
Max. ant.-post. diam., dist. articulation	—	25,6	24,1	22,4	—	—	—	21,9	—	—	—
Max. transv. diam., dist. articulation	—	28,1	26,0	c. 23,0	—	—	—	23,7	—	—	—

No complete innominate of *A. africanum* is known, the best specimen (L33341) comprising only the posterior part of the ilium and the acetabular region. The latter is similar to that of the *U. arctos* comparative specimen, and is distinguished only by its slightly larger size. There is, however, a greater dorsoventral constriction of the ilium anterior to the acetabulum, while the dorsoventral diameter of the posterior parts of the sacroiliac articulation is actually less than in the comparative specimen. *A. africanum* is more like *Ailuropoda* in this respect (see Davis 1964, fig. 59). The iliopectineal eminence is less prominent than in *U. arctos*, and in this respect it is also *Ailuropoda*-like. No other important features are observable in L33341, but the fact that it is more like *Ailuropoda* than *U. arctos* in at least two respects may be significant. The pelvis of the former is very different from those of other bears (Davis 1964: 113), and it is possible that that of *A. africanum* was equally distinctive.

The femur of *A. africanum* is represented by several fragmentary specimens, and a complete one (L40002) belonging to an aged and arthritic female (Fig. 20, Table 9). The latter specimen is considerably smaller and more slender than corresponding parts of male specimens, but is morphologically similar to them. It differs from the femur of the *U. arctos* comparative specimen in being slightly longer and relatively more slender.

The head of the femur is hemispherical, as in other ursids, while the neck is distinct and slightly longer than in *U. arctos*, but similar to that of Asian *Euarctos* and *Ailuropoda*. The greater trochanter is lower than the head and it is similar to the *U. arctos* femur in this respect. The gluteal tuberosity is very prominent in L40002 and terminates well below the level of the lesser trochanter, which is also prominent. The area of attachment of the quadratus femoris muscle between the lesser trochanter and gluteal tuberosity is well marked, as is the area of attachment of the adductor muscle, which extends about three-quarters the length of the very straight shaft. The distal end of the femur is essentially similar to that of *U. arctos*.

The femur of *A. africanum* is very different from that identified with *A. sivalense* by Lydekker (1884, pl. 29, fig. 1). This very curious specimen may be pathological.

The tibia of *A. africanum*, of which only one complete specimen (L45062) is known, is also very variable in size (Fig. 21, Table 9). As with the femur, L40002, the tibia is longer than that of the *U. arctos* comparative specimen, but in this instance it is also much stouter, evidently because L45062 belongs to a male. The proximal end of the tibia differs most markedly from those of ursines in having the tibial tuberosity and crest more prominent. This applies even in the case of specimens belonging to females (e.g. L50842). In addition, the proximal articular facets are relatively longer anteroposteriorly.

In *Ailuropoda* and ursines the lateral edge of the tibia shaft viewed anteriorly is bowed, with the tibial crest paralleling the proximal curvature. This, together with prominent lateral projections at the proximal and distal ends, 'increases the interosseous space between the tibia and fibula, and the total width across



Fig. 20. A-B. Anterior and posterior views of Langebaanweg *Agriotherium* femora.
A. L40002. B. L40128. C. Medial view of L40002.



Fig. 21. Anterior and medial views of Langebaanweg *Agriotherium* tibia, L45062.

TABLE 9
Dimensions of Langebaanweg *Agriotherium* femora and tibiae.

	FEMORA				TIBIAE			
	L40043	L40128	L40002	L49889	L50841/ L50833	L45062	L40029	L40028
Overall length	—	—	425,0	—	—	378,0	—	—
Max. ant.-post. diam. of head	c. 57,5	54,1	48,4	—	—	—	—	—
Max. ant.-post. diam., proximal end	—	—	—	—	—	98,1	87,3	85,7
Max. transv. diam., proximal end	c. 128,0	111,5	98,0	—	108,5	100,1	c. 93,0	c. 91,0
Max. ant.-post. diam., distal end	—	—	76,7	71,0	52,1	51,0	—	—
Max. transv. diam., distal end	—	—	c. 82,0	71,2	72,0	65,0	—	—



Fig. 22. Tarsal bones of Langebaanweg *Agriotherium*, L45062. A. Proximal, lateral, ventral and distal views of astragalus. B. Lateral and dorsal views of calcaneum. C. Dorsal view of cuboid. D. Proximal view of navicular.

the leg' (Davis 1964: 115). The tibia of *A. africanum* differs in having the proximal and distal lateral projections less prominent, and the shaft less bowed, which gives it a much straighter and more bilaterally symmetrical appearance in anterior view. The distal articular facet, like the proximal ones, has a relatively greater anteroposterior diameter than in ursines. The same applies to the proximal and distal fibula facets, while the fibula itself is much like those of ursines.

All the tarsal bones of *A. africanum*, except the mesocuneiform, ectocuneiform and tibial sesamoid, are known from at least one, and as many as eight specimens (Fig. 22, Table 10). The tibial sesamoid, like the radial sesamoid, was probably absent in this species. As with the carpals, the tarsals are essentially similar to their counterparts in Ursinae, and they, too, exhibit appreciable sexual dimorphism.

The astragalus is the best represented tarsal bone. It is distinguished from those of ursines principally by a longer neck. The available ursine astragali have a variably developed lip of bone projecting posteriorly from the base of the tibial facet, and which is most prominent medially. This lip of bone is absent in *A. africanum*, although in the specimens L45062 and L47533 there is a ventrally projecting lip of bone in this position. Since it effectively inhibits movement between astragalus and calcaneum, it is probably an abnormality caused by osteo-arthritis.

The calcaneum of *A. africanum* is also ursine-like, differing principally in having a relatively shorter and much stouter tuber calcis.

The remaining tarsal bones differ in only minor respects from their counterparts in *U. arctos*.

All the metatarsals of *A. africanum* are represented by at least one complete specimen (Fig. 23, Table 11). They are in general much stouter but only slightly longer than their counterparts in *U. arctos*. An exception is a small metatarsal I (L50771), evidently that of a female, which is of similar length and which is

TABLE 10
Dimensions of Langebaanweg *Agriotherium* tarsals.

	ASTRAGALI					
	L45062 (R)	L50765	L47533	L50766	L50770	L47910
Max. ant.-post. diam.	63,6	—	61,9	58,0	46,7	45,8
Max. transv. diam.	63,2	62,1	59,8	c. 56,5	51,2	43,7
Transv. diam. of tibial facet	44,9	c. 46,0	43,1	37,2	33,5	29,5
Transv. diam. of navicular facet	43,5	44,5	43,0	37,9	32,8	27,0
Max. dorsoventral diam.	40,4	—	37,2	35,3	28,8	27,5
	CALCANEUM		NAVICULARS		CUBOID	
	L45062		L50773	L45062	L45062	
Max. ant.-post. diam.	100,0		48,7	43,3	42,2	
Max. transv. diam.	64,5		38,7	38,2	34,9	
Max. dorsoventral diam.	56,4		20,5	17,6	35,9	
Max. transv. diam. of tuber calcis	45,7		—	—	—	

(R) = Right

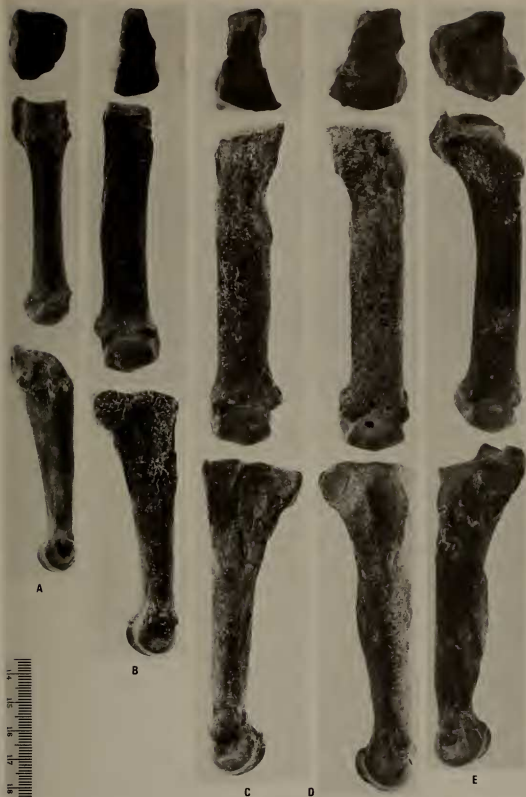


Fig. 23. Proximal, anterior and lateral or medial views of Langebaanweg *Agriotherium* metatarsals. A. I, L50787. B-E. II-V, L45062.

TABLE 11
Dimensions of Langebaanweg *Agriotherium* metatarsals.

	I			II			III	
	L50787	L47387	L50771	L48573	L45062	L40030	L45062	L30205
Overall length	81,5	—	70,1	103,1	94,4	92,0	110,6	107,9
Max. ant.-post. diam., proximal end	23,6	22,8	21,7	32,3	32,0	30,0	36,5	34,1
Max. transv. diam., proximal end	22,1	21,7	19,6	17,8	17,3	17,0	24,2	22,5
Max. ant.-post. diam., distal articulation	14,3	—	13,0	18,0	18,2	17,1	20,5	19,4
Max. transv. diam., distal articulation	17,5	—	14,4	20,7	21,2	19,6	22,2	21,1
	IV		L50812	V		L50829	L41108	
	L50824	L45062		L48572	L45062			
Overall length	—	116,4	—	119,5	115,5	—	—	—
Max. ant.-post. diam., proximal end	39,2	35,4	32,1	31,1	30,8	29,6	27,3	—
Max. transv. diam., proximal end	31,8	27,9	32,3	27,0	30,7	31,1	27,5	—
Max. ant.-post. diam., distal articulation	—	20,6	—	19,7	21,0	—	—	—
Max. transv. diam., distal articulation	—	23,7	—	c. 22,5	23,2	—	—	—

more slender than that of the *U. arctos* comparative specimen. Morphologically there are no significant differences between the metatarsals of *A. africanum* and *U. arctos*.

The patella, sesamoids and phalanges of *A. africanum* are also *U. arctos*-like, although the 1st and 2nd phalanges of the former are relatively much shorter and stouter (Fig. 24).



Fig. 24. Dorsal and lateral or medial views of Langebaanweg *Agriotherium* phalanges, L45062, possibly of one digit.

DISCUSSION

The overall impression gained from the study of the skull and postcranial skeleton of *A. africanum* is of a large and heavily built animal which was unmistakably bear-like in its appearance (Fig. 25). It was undoubtedly plantigrade since its postcranial bones exhibit most of the characteristics found by Ginsburg (1961) to be indicative of this condition. The appreciable size variation observed is to be expected of a bear of such large proportions, since marked sexual dimorphism is characteristic of these animals (Kurtén 1955, 1966, 1967). Being typical of large ursids in this respect, it is of interest to compare *A. africanum* with better known species which belong in this category. They include *Ursus spelaeus*, *Tremarctos floridanus*, and *Arctodus simus*.

Of these species *A. africanum* probably resembled the North American late Pleistocene tremarctine, *Arctodus simus*, most closely. For example Kurtén (1967: 49, fig. 28) found that the skull of this short-faced bear 'shows a remarkable convergence with the great cats', which is also a feature of the skull of *A. africanum* (see p. 9 and Fig. 3). In overall size the male skull of the latter (L45062) is intermediate between those of female and male *A. simus* (see Table 1 herein and Kurtén 1967, table 5). In addition, the postcranial bones of *A. africanum* are similar in proportions to those of *A. simus*, although they differ in

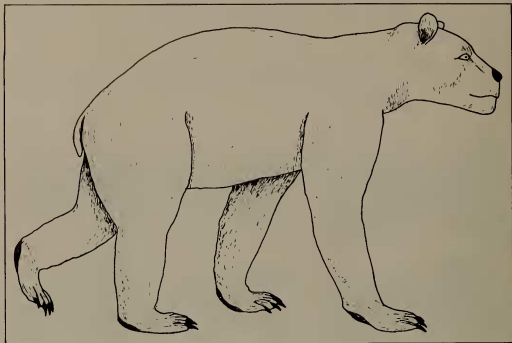


Fig. 25. Reconstruction of *Agriotherium*, adapted from one of North American *Arctodus simus* by J. Matternes (in Guthrie 1972).

some morphological details. In actual size the bones of *A. africanum* males compare closely with those of *A. simus* females (e.g. the Potter Creek Cave sample—see Tables 4–11 herein and Kurtén 1967, tables 10–25).

Unfortunately the skeleton of *A. africanum* is less well represented than that of *A. simus* and consequently cannot be analysed in as much detail. In view of the marked individual size variation in *A. africanum* it may be misleading to combine skeletal elements of different individuals in metric analyses. Nevertheless, this was done in several instances, one of which is presented here.

The isolated metatarsal I, L50787, which is evidently that of a male, was combined with the metatarsals II to V of L45062, also a male, in order to compare their relative lengths with the metatarsals of other ursids (Table 12). The similarity to the Potter Creek Cave *A. simus* sample is striking.

On the other hand, the calcaneum length expressed as a percentage of the longest metatarsal length of L45062 is 86.6, a figure which compares closely with the 86.5 of an *U. arctos* sample, and which is considerably lower than the figures for extinct tremarctines and *U. spelaeus*, which are over 100 (Kurtén 1966, table 36; 1967, table 27).

In spite of such deviations from the *Arctodus* pattern, *A. africanum* is like this genus and different from other later ursids in having relatively long legs. This characteristic, together with its specialized skull and dentition, is a highly significant departure from the typical ursid condition. Kurtén (1967: 50) interpreted *A. simus* as 'a predominantly carnivorous form', which may have

TABLE 12

Relative lengths of the metatarsals of some bears expressed as a percentage of the length of metatarsal V.

	I	II	III	IV	V
<i>Agriotherium africanum</i> . . . (L50787 + L45062)	71	82	96	101	100
<i>Arctodus simus</i> ¹ (Potter Creek Cave)	70	82	95	99	100
<i>Tremarctos floridanus</i> ¹ (males)	69	80	91	103	100
<i>Ursus spelaeus</i> ¹ (Salzofen)	63	78	88	98	100
<i>Ursus arctos</i> ¹ (Recent)	65	79	87	96	100

¹ Kurtén 1967, table 26.

'preyed on large contemporary herbivores', and although not 'truly cursorial it may have been capable of bursts of speed exceeding those of *U. arctos*'. These conclusions presumably apply equally well in the case of *A. africanum*.

The ecology and relationships of this species will be dealt with in more detail in following sections of this report.

PALAEOECOLOGY

The Langebaanweg *Agriotherium* assemblage is comprised of over 330 specimens, which represent a minimum of 14 individuals. Females are much less commonly represented than males, and no very young animals are known. Those postcranial bones belonging to immature individuals are probably all of young adults, while those of which teeth are known are all young or prime adults. Some specimens (e.g. L40002) show signs of osteo-arthritis, which suggests an advanced age for the individuals concerned. Bone pathology is otherwise rare, one notable exception being the metacarpal, L45448, which exhibits an osteitis of the proximal end, the cause of which is unknown.

All *A. africanum* specimens were found in, or closely associated with, river channel deposits. They occurred together with a wide variety of terrestrial, freshwater and marine vertebrates, which range in size from shrews to whales. Lists of most associated mammals have been given elsewhere (Hendey 1976, table 4; 1978, table 10). Associated birds will be listed by P.V. Rich (in preparation). Lists of lower vertebrates, which include cartilaginous and bony fish, amphibians and reptiles, have yet to be compiled. It is clear that *A. africanum* was an element of a rich and diverse fauna, with resemblances to both late Miocene (Turolian) faunas of Eurasia, and later African faunas. The Varswater Formation fauna includes descendants of taxa typical of the Eurasian late Miocene, with *A. africanum* included in this category, as well as ancestors of species which are now typically African.

A. africanum is one of the Varswater Formation taxa not recorded from the Quartzose Sand Member, the lowest of the three important fossil mammal-bearing units of the succession (Hendey 1976) (Table 13). The Quartzose Sand

TABLE 13

Depositional environments, characteristic sediments and fossil occurrences in the Varswater Formation, 'E' Quarry, Langebaanweg.

Dingle <i>et al.</i> 1979	Hendey 1976 and this report		DEPOSITIONAL ENVIRONMENTS	CHARACTERISTIC SEDIMENTS	FOSSIL OCCURRENCES
A-C D1	PPM, undifferentiated		marine littoral	phosphatic sand	some marine microfossils, vertebrates very rare
	D3	I	river bank	clayey sand on phosphate rock	fossils abundant; seals and terrestrial vertebrates predominant
II		river channel	quartz sand and fossil lag on, and in lee of phosphate rock	fossils abundant; seals and terrestrial vertebrates predominant	
III		intermediate between II and IV	quartz sand and fossil lag grading into carbonaceous sand and clay	fossils common; seals and terrestrial vertebrates predominant	
D2	IV	marsh and pond	carbonaceous sand and clay, sometimes under quartz sand and clay horizons	fossils progressively less common south of III; only vertebrates recorded, but pollens probably present	
D4	PPM, bed sub-divided 3aS		river channel and river bank	quartz sand and fossil lag grading upwards into phosphatic sand	fossils abundant, but becoming less common in phosphatic sand; terrestrial vertebrates predominant

E1 E2 E3 E4 F	QUARTZOSE SAND MEMBER		I I(A) II III (IV) GM, undifferentiated	floodplain, with associated microenvironments (e.g. pond, minor drainage channel) possible variation of I, ? flood- plain closer to river channel marsh tidal flats ? river channel (not exposed but probably exists south-east and south of quarry) rocky and sandy beach	quartz sand quartz sand carbonaceous sand and clay muddy silt not known phosphate rock gravel and quartz sand	fossils sometimes abundant; terrestrial vertebrates predominant fossils sometimes common; terrestrial vertebrates predominant fossils abundant; pollens pre- dominant, terrestrial vertebrates common fossils abundant; marine, estu- arine and freshwater inverte- brates predominant not known fossils sometimes abundant; marine vertebrates and inverte- brates predominant
GRAVEL MEMBER						

Note. The subdivisions D2 and D3 and E1 to E4 (and their equivalents, PPM 3aI to IV and QSM I to IV) are facies of sedimentary units (see Dingle *et al.* 1979, fig. 5).

Member deposits were laid down mostly on the floodplain of a river which then met the sea to the south or south-west of the existing 'E' Quarry. Many of the fossils from this unit are believed to represent the remains of animals which lived in the immediate vicinity (Hendey 1974: 349-353; 1976: 223-226). By contrast, most of the Pelletal Phosphorite Member fossils, including those of *A. africanum*, were washed into the area by the river, which was then following more northerly courses, first depositing bed 3aS and later bed 3aN (Hendey 1976: 226-230). Consequently, the *A. africanum* fossils are likely to be out of their natural environmental context, and there is no way of certainly establishing the nature of the preferred habitat of the species. Assuming that *A. africanum* was a terrestrial species, the number of possibilities is, however, limited, and there is some evidence which favours one of them.

The environment in the vicinity of Langebaanweg and in adjacent areas at the time of deposition of the Varswater Formation was clearly very different from that of the present (Hendey 1973). Long-necked giraffes (*Giraffa* sp.) were common, and, together with other large browsers such as a sivathere (*Sivatherium hendeyi*), a palaeotragine (*Palaeotragus* cf. *germaini*), and primitive proboscideans (*Anancus* sp., *Mammuthus subplanifrons*), indicate the presence of trees, probably in substantial numbers, and perhaps in the form of a riverine woodland. On the other hand, grazers such as alcelaphine antelopes (Gentry 1980 in press), an equid (*Hipparion* cf. *baardi*), and a rhinoceros (*Ceratotherium praecox*) indicate the presence of grasslands as well. Although there was evidently a variety of micro-environments in the area (Hendey 1976), it is only the major terrestrial habitats of woodlands and grasslands which need be considered in the case of *Agriotherium*.

Of the large herbivores, the one which occurs most commonly in the Quartzose Sand Member and bed 3aS of the Pelletal Phosphorite Member is *Ceratotherium praecox*, a grazer, while browsing giraffoids are very rare in the Quartzose Sand Member, and only slightly more common in bed 3aS. By contrast, *C. praecox* is either very rare, or absent, in bed 3aN, while giraffoids are astonishingly well represented. The implication is that either woodlands became a progressively more widespread habitat during deposition of the Varswater Formation, or that taphonomic factors were such that woodland species had their remains incorporated in the deposits with increasing frequency. Either way, the fact that *A. africanum* is not recorded from the Quartzose Sand Member, is rare in bed 3aS, and is relatively common in bed 3aN, suggests that it was a woodland species.

This conclusion has also been reached in respect of *Agriotherium* elsewhere. Kurtén (1968: 119) suggested that *Agriotherium* 'was probably a forest animal like most modern bears', while Wolff *et al.* (1973: 226) concluded that 'it does seem that specimens of *Indarctos* and *Agriotherium* are better represented at localities which have a greater representation of woodland forms'. The possible influence of habitat on the evolution of *Agriotherium* will be discussed later (see p. 70).

The habitat preference of *Agriotherium* may have been a factor which contributed to its comparatively poor fossil record, but this was almost certainly due largely to the habits of the animal. *Agriotherium* has long been recognized as an atypical ursid because it was apparently carnivorous rather than omnivorous. Carnivorous species of such gigantic proportions would of necessity have been rare animals, even under the most ideal conditions (Wolff *et al.* 1973). The same restriction would not apply in the case of more omnivorous bears, and for later species the 'fossil record is excellent; indeed, as regards the Pleistocene bears of Europe, almost incomparable' (Kurtén 1968: 119). An added factor in the case of the latter was that extreme climatic conditions during the Pleistocene led bears to use caves as retreats, with consequent concentration of their remains in caves. Such circumstances did not apply to *Agriotherium*, all remains of which are recorded from open sites dating from a climatically moderate period.

Although *A. africanum* has been said to be a well represented species, it is nevertheless one of the less common elements in the Langebaanweg assemblage, which is now comprised of the remains of many thousands of animals. Proportionately, *Agriotherium* may be no more common at Langebaanweg than it is at localities elsewhere.

Many of the Langebaanweg *Agriotherium* specimens were recovered in the course of mining operations, or by screening of bulk sediment samples mechanically removed from the mine. In these instances the original condition of specimens, associations of skeletal elements and body part representations cannot necessarily be determined. More significant from a taphonomic point of view is that material recovered from controlled excavations. Three such excavations yielded *Agriotherium* remains (Fig. 26, Table 14), and the relevant material is listed on pages 5-6.

The deposits in which this material occurred are noteworthy for the almost complete absence of a very coarse lithic fraction. Occasional pebbles of quartz, feldspar and the local phosphate rock do occur, but the sediments are generally made up of medium- to coarse-grade sands. Fine sands and clayey sands are also present. The larger elements of the lag gravels in bed 3aN are almost exclusively bones and teeth of vertebrates (Fig. 27). Consequently, those fossils transported by the river were not subjected to the destructive battering by, and against, cobbles and boulders, which is often a feature of this sedimentary environment. For about 30 km east of Langebaanweg there are few rock outcrops, the area being largely covered by the generally sandy deposits of the 'Sandveld' (see Talbot 1947; Visser & Schoch 1973). This means that in its lower reaches the river which was largely responsible for building up the Varswater Formation (Fig. 1) could have picked up little in the way of a coarse lithic fraction. In addition, its generally sandy bed would have provided a relatively smooth passage for organic materials in its load.

In fact the fossils of beds 3aS and 3aN show remarkably few signs of abrasion which could be ascribed to transport in sand-charged water over a



Fig. 26. Aerial view of past and present areas of exposure of bed 3aN in 'E' Quarry, Langebaanweg. 1—LBW-E 1975/1; 2—LBW-E 1976/1; 3—Dump 10; 4—LBW-E 1976/2; 5—Dump 9; 6—Dump 8; 7—Carbonaceous deposits; R—Phosphate rock outcrops; W—Wet season river channel; D—Dry season river channel.

sandy substratum. What abrasion there is may have developed after deposition rather than during transport (see below). This suggests that many of the fossils reached the vicinity of 'E' Quarry still protected by soft tissue, perhaps even as floating carcasses, and that disarticulation and dispersal of skeletal elements took place locally.

The bed 3aN *Agriotherium* specimens were recovered from deposits laid down in three distinct micro-environments. Those deposits exposed in the

TABLE 14

Controlled excavations in 'E' Quarry which yielded *Agriotherium* remains.

EXCAVATION NUMBER	SITE	DEPOSITIONAL ENVIRONMENT	STRATIGRAPHIC UNIT ¹
LBW-E 1975/1	TCWW Prom	river bank and river channel, with phosphate rock substratum	PPM 3aN I
LBW-E 1976/1	RP	river channel, with phosphate rock substratum	PPM 3aN II
LBW-E 1976/2	IWRP ²	river channel in lee of phosphate rock, with unconsolidated sand substratum	PPM 3aN II

¹ See Table 13.² Locality 5 of Dingle *et al.* 1979, fig. 2.

excavation LBW-E 1975/1 were laid down partly in the river channel and partly on the north bank of the channel. Channel deposits were sampled in both excavations LBW-E 1976/1 and 1976/2, the depositional environments differing only in that the former had a rock substratum and the latter a sandy one. In both the 1975/1 and 1976/1 areas the substratum was a phosphate rock horizon of up to 0,75 m thick. The third micro-environment was not sampled by controlled excavation, but was the source of a few *Agriotherium* specimens recovered in the course of mining operations. This was an extensive area of carbonaceous (peat-like) deposit over the southern (seaward) limit of the river channel. It was probably the area of accumulation of plant debris washed down by the river during flood times. During the dry season it formed the west bank of the river and was probably a marshy area with appropriate vegetation. The likely positions of the wet and dry season channels are indicated in Figure 26.

The bed 3aN deposits are overlain by the thick and extensive commercially exploited phosphatic sand, which was deposited in a marine littoral environment (Tankard 1975), and from which some fossil vertebrates, not including *Agriotherium*, are known (Hendey 1976: 230).

The fossils from LBW-E 1975/1, which were deposited close to or on the north bank of the river channel, were generally better preserved and less fragmented than those from the other two excavations. This applied particularly in the case of specimens not in direct contact with the phosphate rock substratum. In the area of LBW-E 1976/1 most of the deposit overlying the phosphate rock had been mined away, and the material recovered came from on, or close to the rock surface itself, particularly depressions therein. This material was for the most part very fragmented.

The greatest concentration of fossils in bed 3aN was in the area of LBW-E 1976/2. Here the deposits were laid down on an unconsolidated substratum (the Quartzose Sand Member) in the lee (west) of the phosphate rock exposed

in the other two excavations. Immediately adjacent to the phosphate rock a 60 cm thick horizon of fossils was accumulated (Fig. 27). This thinned out rapidly to as little as 10 cm westwards and southwards. Most of the fossils in this area were highly fragmented and in a poor state of preservation. This applies particularly in the case of the remains of larger species, of which giraffoids, especially *Sivatherium*, were by far the most commonly represented. By contrast the remains of aquatic vertebrates, with the seal, *Prionodelphis capensis*, being exceedingly common, tended to be in good condition, although their remains were often fragmented and skeletons disarticulated and dispersed.

As this fossil lag deposit thinned westwards and southwards, the clastic matrix became finer-grained, with an increasing clay component. Westwards the fossiliferous horizon terminated abruptly against another phosphate rock outcrop, but southwards it once again thickened and also spread out laterally in a south-westerly direction. There was also a rapid darkening in the colour of the clastic matrix, which coincided with a diminution in the occurrence of vertebrate fossils. These fossils occurred mostly as isolated, and often fragmented, teeth and bones, but associated parts of skeletons, including at least one of *Agriotherium*, are recorded. In the case of the latter, it is not known how complete they were, since all were chance discoveries made after disturbance of the deposit by mechanical excavators.

The darkening of the deposits southwards was caused by an increasing carbonaceous fraction, which was evidently derived from decomposed plant remains. This deposit was not a pure peat, the carbonaceous material having been mixed with a high proportion of sand and clay, but such peats might well have overlain the remaining carbonaceous deposit (see below).

The picture which emerges is that of a river which in times of flood carried in to the area remains of terrestrial vertebrates, sometimes as whole carcasses, depositing some along its banks and others in the channel itself. A major part of the load of vertebrate remains was deposited immediately after the channel passed over the western edge of a southward projecting tongue of phosphate rock. Another such outcrop about 30 m further west then deflected the channel southwards, where it spread out over a wide and flat area. Here it dropped the last of its organic load, this probably being comprised largely of easily transportable plant material. Some vertebrate remains also reached this area, but they are recorded only from the more northerly parts, that is, closest to the area where the main vertebrate load was dropped.

Although the vertebrate assemblage of bed 3aN is comprised largely of the remains of terrestrial species washed in by the river, marine vertebrates are also represented. In the case of the seal the number of individuals involved is substantial. The marine vertebrate remains are generally better preserved than those of terrestrial species, which suggests, not surprisingly, that they had suffered less transport. The seals, cetaceans, marine birds, bony fish, and sharks may all have been inhabitants of, or visitors to, the river estuary. This probably applied particularly during flood times when the influx of carcasses of terrestrial species

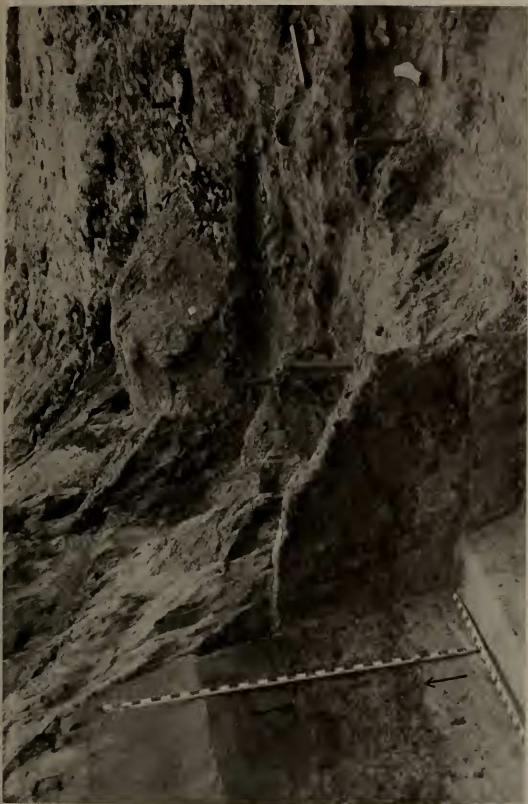


Fig. 27. LBW-E 1976/2 area of 'E' Quarry. Fossil lag deposit arrowed left, and phosphate rock outcrop sloping upwards in a north-easterly direction on the right. Scale in 5 cm divisions.

provided an abundant source of food for marine scavengers. Whether or not the seal was included in this category is not known. Seals may simply have been attracted by an increase in the numbers of scavengers such as fish and crustaceans, and would themselves have attracted predators such as sharks. Marine vertebrates were certainly in a position to have their remains caught up in, and dispersed by, the river's floodwaters.

During the dry season when the river was not in flood it is unlikely to have breached the phosphate rock outcrop which underlies the northerly and easterly parts of bed 3aN. Instead it would have been deflected southwards by this outcrop in the direction of bed 3aS, which was laid down during an earlier phase of the Varswater cyclothem. This would account for the fact that bed 3aS was abruptly truncated south of the phosphate rock outcrop. This truncation was not due solely to flood periods in bed 3aN times because bed 3aS terminated at least 25 m east of the first exposure of the carbonaceous deposit of bed 3aN, which is an indication of the width of the dry season channel. There may have been other distributaries of the river north of 'E' Quarry.

As indicated earlier, that area west of the dry season channel, where floodwaters had dropped their load of organic materials, probably took the form of a marsh.

Although the river probably still fed vertebrate remains into the area during the dry season, the number of specimens involved is likely to have been much lower. This raises a problem in connection with specimens collected between the principal exposures of bed 3aS and bed 3aN. There are relatively few such specimens, and their actual source is usually uncertain, since most were collected by mine workers in the course of their activities. This material has been recorded as being from bed 3aS, but it may actually belong with the bed 3aN complex of deposits. Those *Agriotherium* specimens with numbers between L40000 and L43000 fall into this category.

Fortunately there are no doubts about the source of *Agriotherium* specimens from the bed 3aN excavations, and those from the bed 3aN carbonaceous deposits, the latter being distinctive because of their dark colour. The only other fossils from 'E' Quarry in a similar state of preservation are those from the 'peat bed' of the Quartzose Sand Member (Hendey 1976: 218, table 2), and there was no possibility of material from these two deposits becoming mixed.

Although there can be little or no doubt as to how the bed 3aN *Agriotherium* remains reached the 'E' Quarry area, it is of interest to consider the nature of some of this material.

The partial skeleton, L45062, is interpreted as the remains of an animal which reached the point of its discovery as a complete, or nearly complete carcass. This carcass was deposited about 15 m west of the phosphate rock outcrop in the LBW-E 1976/2 area. It is virtually certain that at least some, and perhaps all, missing parts of L45062 were mined away, the parts recovered having come from an area of 2 to 3 m² immediately adjacent to a vertical face cut by a mechanical excavator. The remains were found in the lag deposit where

it was about 20 cm thick, and were centred on a depression on the unconsolidated substratum. The preservation of the remains was considerably better than that of the majority of surrounding fossils. Their good preservation, together with the unmistakable characteristics of *Agriotherium* bones and teeth, facilitated their recovery from a mass of thousands of fragmentary fossils.

It appears that after deposition of the carcass of L45062, flowing water scoured the depression beneath it. At the same time the carcass acted as an obstruction to coarse debris, causing it to settle in the immediate vicinity. Disarticulation and slight dispersal of skeletal elements followed decomposition of soft tissue. L45062 is unusual in being one of the few instances in the LBW-E 1976/2 area where parts of one individual were found in a good state of preservation, and with skeletal elements in close association. This was otherwise noticeable mainly amongst the seals, although in these instances the large number of individuals involved made it impossible to separate their skeletons.

The *Agriotherium* forelimb, L45063, was another instance where there was association of skeletal elements of one individual. This material was found in the same depression as L45062, but was readily distinguishable, having belonged to a smaller (female) individual. This forelimb must also have reached the area held together by soft tissue, perhaps with the scapula and most phalanges already detached. Although no two elements of this limb were found in articulation, the individual elements were less dispersed than those of L45062. The incomplete manus, L33160, from LBW-E 1975/1, was a similar occurrence to L45063.

Other *Agriotherium* specimens from the bed 3aN controlled excavations tended to be isolated occurrences of individual skeletal elements. Since they are generally well preserved and show few, if any, signs of abrasion, they, too, are likely to be from carcasses similar to that of L45062. However, in these instances there was greater dispersal of skeletal elements and associations were no longer obvious. The condition of isolated specimens was usually in keeping with the nature of the depositional environment. Long bones were invariably fragmented, but shorter and stouter bones, such as those of the manus and pes, were usually intact. The hemimandible, L45114, had lost the single-rooted teeth (incisors, P_3 and M_3), which are easily separated from the jaw, and the ascending ramus, which is more fragile than the mandibular corpus. The single-rooted canine was still in position, because the root of this tooth is large and slightly bulbous, and impossible to remove from the jaw without breaking the root or the bone enclosing it.

Also of interest from a taphonomic point of view is the post-mortem damage to specimens. This was clearly dependent on the micro-environment in which specimens were deposited.

The incomplete manus, L33160, was deposited close to, or on the north bank of the river in the LBW-E 1975/1 area. This specimen is remarkable because it provides evidence of the activities of hyaenas in this area. Like many of the fossils from 'E' Quarry, L33160 shows signs of having been chewed by



Fig. 28. Hyena-gnawed *Agriotherium* manus, L33160, from Langebaanweg. Arrows indicate areas of major damage.

a hyaena, and this was done while the bones were still articulated. The phalanges, metacarpal I and distal ends of the metacarpals II to V are lost, probably having been ingested by the hyaena concerned, and there are tooth-marks on some of the metacarpals adjacent to the missing parts. There is also damage on the scapholunar and unciform, but the magnum and trapezoid, which are largely enclosed by the other bones, are intact (Fig. 28).

The remains of at least six small hyaenas (*Ictitherium preforfex*) were recovered from LBW-E 1975/1. This species of hyaena, and perhaps others, probably scavenged the banks of the river for the remains of animals washed into the area. Hyaena-damaged bone was not uncommon in this area, another notable example being the skull of a seal with double punctate marks on the braincase. The lower canines of *Ictitherium preforfex* fit these punctate marks well.

Another specimen from LBW-E 1975/1, the metatarsal L30205, is remarkable in having on its shaft gnaw-marks apparently made by a small rodent (Fig. 29). This type of damage is rare amongst the fossils from 'E' Quarry.



Fig. 29. Rodent-gnawed *Agriotherium* metatarsal, L30205, from Langebaanweg. Arrow indicates area of damage.

Although rodent remains are generally common in the fossiliferous deposits of the Varswater Formation, this was not the case in the LBW-E 1975/1 area, where only bathyergids were represented in moderate numbers. Living bathyergids, which are fossorial, are known to gnaw at objects encountered in their tunnels, plastic water-pipes and telephone cables being items recently affected in this way in the south-western Cape Province. It is possible that a bathyergid tunnelling on the river bank was responsible for the damage to L30205.

Three distinct types of post-mortem damage are evident on the bones and teeth of the partial skeleton L45062. Most common is simple fracturing of bones, which is ascribed to movement after loss of soft tissue, and to subsequent compression by overlying deposit. Not surprisingly, it was the relatively delicate parts of the skull which were particularly affected by this fracturing. The second type of damage is abrasion, which was probably caused by sand-charged water

flowing over exposed parts of the partly buried skeleton. This type of damage is not uncommon on the fossils from 'E' Quarry, and a good example was mentioned elsewhere (Hendey 1970: 82, fig. 3).

The third type of damage was caused by fire, with affected bones and teeth being blackened, more badly fractured and less well preserved than unburnt bone (Fig. 30). This type of damage is also not uncommon on fossils from 'E' Quarry, and has been discussed elsewhere (Hendey 1974: 351; 1976: 224).



Fig. 30. Fire-damaged *Agriotherium* astragalus, L45062, from Langebaanweg.

It was previously assumed that fire-damage was caused by dry-season bush or grass fires. While this may sometimes have been the case, there are instances where the inferred depositional environment and nature of the damage is such that fires of another sort are likely to have been responsible. The fire-damage of L45062 is a case in point.

It is clear that this damage was done after the skeleton had been disarticulated, since severe fire-damage on one bone is not matched by damage to immediately adjacent parts of the skeleton. For example, the symphyseal region of the right hemimandible is fire-damaged and the incisors are lost, whereas the left hemimandible is intact in this region and the incisors are present. Similarly, the distal end and part of the shaft of the left ulna is damaged, but corresponding parts of the left radius are unaffected.

Assuming that the depositional environment of L45062 has been correctly interpreted, it is highly improbable, if not impossible that the random burning of parts of the skeleton could have been caused by a bush or grass fire. A more plausible explanation is that the fire-damage was caused by peat fires, a phenomenon which has been reported in a North American estuarine swamp by Staub & Cohen (1979). It was indicated earlier that the horizon in which L45062 occurred graded laterally into a peat-like deposit, and that pure peats may have overlain this horizon. Such peats, if they did exist, may have been prone to dry season fires like the American example cited above. Having burnt away they would have left no trace obvious to observers unfamiliar with such phenomena other than some underlying burnt bone.

Peat fires may also have led to the formation of hitherto unexplained deposits capping the peat-like sediments immediately south of the LBW-E 1976/2 area. Immediately overlying the 'peat' was a horizon of sand a few centimetres thick, which was recorded as being 'orange-brown' in colour and in this respect unlike any other sand body recorded before or since in 'E' Quarry. The 'orange-brown sand' was in turn overlain by a grey clay incorporating scattered sand grains. In the examples of peat fires recorded by Staub & Cohen (1979), and in other similar ones (e.g. Cypert 1961), ponds developed in depressions left in the peat after burning, and such ponds become a new and distinct depositional environment in the areas in question. If there was, indeed, a peat fire in the LBW-E 1976/2 area, the orange-brown sand and grey clay may represent sediment accumulated in a resultant pond, while the underlying carbonaceous deposit represents an unburnt residue of the original peat deposit. The carbonaceous deposit may have remained unburnt either because it was waterlogged or because its high non-carbonaceous content made it incombustible.

The grey clay is finely laminated, suggesting slow accumulation in still-water conditions, with individual sediment particles perhaps having been transported to the pond by wind. The origin of the orange-brown sand is not known. It was initially thought that it may represent the unburnt residue of the peat fire, but the occasional vertebrate fossils incorporated in the sand show no signs of having been burnt.

The existence and effects of peat fires at Langebaanweg are largely speculative, but they do provide a plausible explanation for hitherto unexplained, or unsatisfactorily explained, aspects of the fossils and the deposits.

The ecological role of *Agriotherium* is also relevant here. It was mentioned earlier that *Agriotherium* was a carnivorous animal and, judging from its dentition, it was better adapted to carnivory than almost all other later ursids. It is the nature of the posterior cheek teeth which are particularly significant in this respect, and since these teeth are better represented in *A. africanum* than in previously recorded *Agriotherium*, it is useful to examine them from a functional viewpoint.

The P⁴, M¹ and M² of *A. africanum*, and other *Agriotherium*, resemble one

another in having a series of prominent buccal cusps and less prominent lingual ones (Fig. 31). In all there are seven buccal cusps, three on P^4 and two on each of the molars, and they are in the form of a smooth curve, with the convexity directed buccally. In addition to being lower-crowned, the lingual cusps are less distinct and fewer in number, only five excluding the vestigial accessory cusps on the P^4 protocone lobe. These cusps are more or less in a straight line.

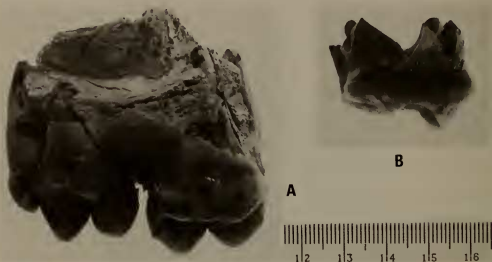


Fig. 31. Langebaanweg *Agriotherium* specimens showing prominence of buccal cusps. A. Lingual view of P^4 and M^1 . B. Anterior view of M^2 .

Judging from wear facets, the buccal cusps have a combined shearing and crushing function, with the former being predominant. The lingual cusps also have this double function, but in this instance the crushing function is predominant.

Much the same applies in the case of P_4 and the lower molars, in which the more prominent cusps are situated buccally. An exception is the large posterolingual cusp of the M_1 talonid. This cusp is, however, like the more buccal ones in developing an inclined shearing facet on its buccal side. The other lower teeth or cusps which develop inclined shearing facets buccally are the paraconid, protoconid and hypoconid of M_1 , the protoconid and hypoconid of M_2 , and the anterobuccal part of M_3 .

A most significant development relating to the emphasis of the buccal cusps in *A. africanum* is the reduction or loss of the anterolingual cusps of the M_2 's, L45114/L46563 and L50007. As far as is known this has not previously been observed in *Agriotherium*. It creates the impression that the M_2 of *A. africanum* was tending to become a second lower carnassial. Although smaller than the true carnassial, L45114/L46563 and L 50007 resemble this tooth in having the trigonid large and functioning essentially as a shearing element.

To have carried this evolutionary experiment to its logical conclusion

would have required continued suppression of the lingual cusps of P⁴, M¹ and M², continued emphasis of the buccal cusps of these teeth, and a similar emphasis on the more buccal parts of the lower molars. This would have resulted in a sectorial dentition unique amongst Carnivora, but since no *Agriotherium* is known in which there was an advance on the *A. africanum* condition, it evidently served the needs of the genus adequately.

It is worth noting in this connection that a similar evolutionary path has been followed by the polar bear, *Thalarctos maritimus*. In this species the P⁴ protocone is reduced or absent, the buccal cusps of M¹ and M² are relatively higher crowned than those of other ursines, while the lingual ones, including the M² talon, are correspondingly reduced. These dental characters reflect 'the carnivorous habits of the species and diverges from the omnivorous dentition of most other ursids' (Kurtén 1964: 4).

Whether *Agriotherium* was a predator or a scavenger is not known. Its large and cumbersome build suggests that the former alternative is less likely, although it may have been capable of hunting down at least some of the larger contemporary herbivores, such as the giraffids. The P⁴ of *Agriotherium* has long been referred to as hyaenid-like (Falconer & Cautley 1836; Wagner 1837), and recently Wolff (1978: 4) has written that this tooth 'bears a striking resemblance in robustness to the teeth of the bonecrushing hyaenas'. This implies a belief that *Agriotherium* may have been a scavenger. However, in the hyaenas it is the more anterior cheek teeth which are enlarged to perform a bone-crushing function, and the enlarged cheek teeth of *Agriotherium* may have been too posteriorly situated to perform this function efficiently.

Irrespective of how its food was acquired, there can be no doubt that an abundance must have been available in the Langebaanweg area when it was inhabited by *Agriotherium*. There is evidence, however, which suggests that the Varswater Formation fauna dates from the latter part of the period which Kurtén (1971: 152) termed the 'climax of the Age of Mammals', and that even in its heyday it was becoming an anachronism. In fact, it is possible that the circumstances which led to the evolution of *Agriotherium* ultimately also caused its extinction.

The late Tertiary was a period of world-wide environmental change, with a general lowering of mean annual temperatures (Butzer 1971, fig. 2), which heralded the glacial-interglacial oscillations of the Pleistocene. Over wide areas of the Old World and the Americas, forests and woodlands were giving way to savannas and grasslands, and these changes had a profound effect on the character and composition of terrestrial vertebrate faunas (Webb 1977).

The Varswater Formation fauna provides evidence of these changes. For example, it includes two of the earliest alcelaphine antelopes yet recorded (Gentry 1980), and it is these bovids with their high-crowned teeth which are characteristic of the African savannas today. Similarly, an early ancestor of Africa's grazing rhinoceros (*Ceratotherium simum*) is recorded from Langebaanweg (Hooijer 1972). Palynological evidence from Langebaanweg, and elsewhere

in the south-western Cape Province, indicates that the modern Cape macchia (fynbos) vegetation was becoming established at this time, and that the climate was changing from 'Cool Wet' to 'Colder Drier' (Coetzee 1978: 121, fig. 2). There is even some as yet unpublished evidence to suggest that there was a marked fall in local sea temperatures during deposition of the Varswater Formation.

The immediate cause of the climatic and environmental deterioration in the Langebaanweg area and adjacent regions was the development of the Benguela Current System off the west coast of southern Africa and the consequent aridification of the adjacent land mass (Siesser 1978; Tankard & Rogers 1978). The development of the Benguela Current was in turn the result of major glaciation in Antarctica later in the Miocene (Kennett *et al.* 1975).

This period of climatic and environmental change must have influenced the Ursidae as much as any other mammalian group. During the Vallesian the ursids which inhabited Europe were generally relatively small omnivorous animals inhabiting forests and woodlands. That lineage which was to give rise to the Ursinae, and probably also the Tremarctinae, continued to be represented by small species during the Turolian. However, in the *Indarctos* lineage there was a marked increase in the size of the species during this period. In the following section of this report, evidence will be presented which indicates that *Indarctos* was the ancestor of *Agriotherium*, and consequently it is the *Indarctos* lineage, and the changes it underwent, which are relevant here.

By the Turolian (and its equivalents) the environment in mid-latitudes was in the process of change, with woodlands giving way to more open country (Kurtén 1971). Consequently, woodland plant foods such as fruits, nuts and berries, favoured by omnivorous ursids, were probably becoming less readily available. It is the larger species which would have been most adversely affected by this development, and thus Turolian *Indarctos*, and its counterparts elsewhere, may increasingly have been forced to adapt their diets to more abundant food sources. In this instance, the response was evidently in the direction of increased carnivory, with adaptations culminating in the evolution of *Agriotherium*.

During the Pleistocene a similar situation arose in respect of *Thalarctos*. At the onset of one of the glaciations, populations of *Ursus arctos* did not retreat southwards in advance of the ice, but instead adapted to the new conditions. Amongst other things, this involved a growing reliance on carnivory to replace the plant foods which had previously been part of its diet (Kurtén 1964; Hendey 1972).

The early ancestors of the giant panda, *Ailuropoda*, evidently responded to late Tertiary environmental change in a different way. They adapted their diet to include more readily available plant foods which had not necessarily figured in their diets previously. Thus arose the most herbivorous of all living ursids, whose main diet of bamboo shoots is varied by other plant foods when this is possible (Ewer 1973).



Fig. 32. The Chemfos Ltd mine property, Langebaanweg, Spring 1970.

By becoming a highly specialized herbivore, *Ailuropoda* ensured its survival, although latterly in diminishing numbers and in increasingly remote areas. On the other hand, by adopting carnivory, *Agriotherium* placed itself in direct competition with smaller and better adapted predators and scavengers for a declining food source (i.e. large woodland browsers), or one which was increasingly difficult for a large ambulatory carnivore to acquire (i.e. cursorial grazers of the savannas and grasslands). According to this hypothesis, the fate of *Agriotherium* was sealed by the factors which led to its origins.

The picture of the Langebaanweg *Agriotherium* which emerges is of a gigantic carnivore living at a time when vertebrate life flourished in the south-western Cape Province, and when the Langebaanweg area was well-watered and richly vegetated. The semi-arid environment of Langebaanweg today, devoid of indigenous trees and scarred by man's activities, is a poor reflection of the past (Fig. 32). Only some of the smallest of the carnivorous cousins of *Agriotherium*, namely foxes, polecats, mongooses and wildcats, still occupy the area and the prospects for their survival are limited.

RELATIONSHIPS OF *AGRIOTHERIUM*

The first *Agriotherium* specimens to be collected and recorded were several isolated teeth of an aged individual found at Montpellier in France early in the nineteenth century. These specimens, which are preserved in the Museum d'Histoire Naturelle, Geneva, were described by Cuvier (1822) under the name of '*Lophiodon* de Montpellier'. Stehlin (1907) gave an account of this historic material, whose true identity remained a mystery for many decades, and provided an indication of the difficulties originally encountered in correctly identifying and classifying specimens belonging to *Agriotherium*.

Although its ursid affinities were recognized by Falconer & Cautley (1836) on the basis of material from the Siwalik Hills of India, *Agriotherium* is in many respects an atypical member of the family. Of all the genera of Ursidae, it is *Agriotherium* and its herbivorous counterpart, *Ailuropoda*, whose relationships have been most controversial. The fact that *Agriotherium* has a poor fossil record, while that of its nearest relatives is not necessarily any better, has aggravated the problem. In addition, there has been a tendency to compare it with the ursine bears, which have long been well known, and this has further obscured matters, since the ursines and *Agriotherium* are only distantly related. Much the same applies in the case of *Ailuropoda*.

Hyaenarctos Owen, 1845, a junior synonym of *Agriotherium* Wagner, 1837, was the generic name in common use during the last century and the earlier part of the present one. Prior to the identification of *Indarctos* by Pilgrim (1913), '*Hyaenarctos*' was the name applied to species now referred to both *Agriotherium* and *Indarctos*. This is an indication that these two genera have many characters in common, a point made obvious by studies such as those of Frick (1926) and Matthew (1929). Pilgrim (1931, 1932) did much to clarify the situa-

tion, and thereafter, apart from occasional lapses (e.g. Viret 1939), the name '*Hyaenarctos*' fell into disuse, and Pilgrim's interpretation of the genera *Agriotherium* and *Indarctos* was generally accepted.

Pilgrim (1932: 42, 43) listed half a dozen characters which he believed distinguished these genera and concluded that '*Indarctos* appears to represent a distinct line of development from *Agriotherium*, in some ways more and in others less advanced than the latter', while '*I. punjabensis* seems to some extent to bridge over the gulf between [them]'. In spite of the attention given by Pilgrim to the problem of distinguishing *Agriotherium* from *Indarctos*, and in determining their relationships to one another, and to other ursids, uncertainties have remained. Nevertheless, it has become common practice to include these genera in the subfamily Agriotheriinae, together with 'the basal genus of the family, *Ursavus*' (Kurtén 1966: 7).

Since *Agriotherium* and *Indarctos* fossils are not common, they, and the question of their relationships, have received only infrequent attention since Pilgrim's (1932) review. Such attention has been prompted on the one hand by descriptions of new material (e.g. Viret 1939; Kretzoi 1942; Tobien 1955; Thenius 1959; Hendey 1972; Crusafont & Kurtén 1976; Wolff 1978), and on the other by reviews of ursid inter-relationships and phylogeny (e.g. Erdbrink 1953; Thenius & Hofer 1960). On those rare occasions when the relationship between *Agriotherium* and *Indarctos* has been discussed, Pilgrim's (1932) opinion has been favoured. For example, both Erdbrink (1953, fig. 61) and Thenius & Hofer (1960, figs. 34-35) place these genera on separate lineages, and indicate derivation from an unknown common ancestor in the *Ursavus* group.

This theory is based on the belief that *Agriotherium* is the more 'primitive' (i.e. canid-like) of the two genera, which, since it survived later than *Indarctos*, must represent a distinct lineage. However, there is an alternative hypothesis. In previous studies on the Langebaanweg *Agriotherium* it was suggested that this genus was directly descended from *Indarctos* (Hendey 1972, 1977), an idea which was apparently first conceived by Schlosser (1899). Before examining this alternative in more detail it is worth noting what is known of the temporal ranges of the two genera.

In Europe *Agriotherium* is first recorded from the Ruscinian, while *Indarctos* is known only from the Vallesian and Turolian (Table 15). In North America *Agriotherium* is restricted to the late Hemphillian (i.e. 4.5-6.0 Ma) and *Indarctos* is recorded only from the latter part of the early Hemphillian (i.e. 6-7 Ma) (R. H. Tedford 1979, pers. comm.). In Africa the Langebaanweg *Agriotherium* is from a Ruscinian-equivalent fauna whereas the cf. *Agriotherium* from Sahabi (Boaz *et al.* 1979) is probably an advanced *Indarctos* in terms of current definitions, and is almost certainly a little older than the Langebaanweg species. The situation in Asia is still obscure, although it is now known that the Dhok Pathan of the Siwaliks, from which important *Indarctos* and *Agriotherium* specimens are recorded, spans an appreciable period during the late Miocene

TABLE 15

The occurrence of *Indarctos* and *Agriotherium* in Europe and the Middle East.

TAXON	LOCALITY	MAMMAL AGE ¹	MEIN ZONE ²	APPROX. AGE IN m.y. ¹
<i>Agriotherium insigne</i>	Montpellier	Ruscinian	14	5
<i>Indarctos atticus</i>	Concud	Turolian	—	9
	Samos		12/13	7-9
	Pikermi		12	9
	Maragha		—	7-8
<i>Indarctos arctoides</i>	Montredon	Late Vallesian	10	10-11
	Orignac		—	—
	Pfaffstetten		—	—
	Westhofen		—	—
<i>Indarctos vireti</i>	Can Llobateres	Early Vallesian	9	12
	Can Purull		—	—

¹ Berggren & Van Couvering 1974; ² Mein 1975.

and Pliocene (Pilbeam *et al.* 1977). Consequently, the Dhok Pathan representatives of these genera, whose taxonomy is controversial (see below), were not necessarily contemporaneous with one another. A similar situation may well exist in the case of *Indarctos* and *Agriotherium* from Chinese late Tertiary localities, with the former known from Localities 30, 31, 43 and 52, while *Agriotherium* is tentatively identified from Locality 13 (Kurtén 1952).

Indications are, therefore, that *Agriotherium* and *Indarctos* were not contemporaries, and when their age is known the former appears later in the fossil record. Consequently, their known temporal ranges are in accord with the theory that *Agriotherium* was descended from *Indarctos*.

While its relationships to *Agriotherium* may be controversial, the history of *Indarctos* itself is now reasonably well documented. It apparently had its origins in Europe during the Vallesian, having stemmed from an *Ursavus*, and subsequently spread through Asia and into North America (Thenius & Hofer 1960), as well as to Africa (see above). Differing interpretations of inter-generic relationships are possible. For example, Crusafont & Kurtén (1976) suggested that *I. vireti* was ancestral to both *I. arctoides* and *I. atticus*, whereas *I. arctoides* is here regarded as an intermediate between the other two species. Crusafont & Kurtén (1976: 15) further suggested that *I. anthracitis* 'may be a precociously specialized form'. This species is, indeed, unusual, perhaps because it evolved in isolation on a Tethyan island, but it is largely irrelevant to present considerations. Recorded Asiatic *Indarctos* are either close to *I. atticus* or more advanced, while North American *Indarctos* is more advanced than *I. atticus*.

Irrespective of the actual inter-relationships of *Indarctos* species, there is no doubt that *I. vireti* is a generalized and early form, whereas *I. atticus*, and Asian and North American *Indarctos* are more specialized and younger in age. For example, Crusafont & Kurtén (1976: 15) noted that *I. atticus* is 'more advanced [than other European *Indarctos*] with larger cheek teeth, more reduced premolars, heavy and powerful jaws, and ursine limb proportions'.

It follows that if *Agriotherium* were descended from *Indarctos*, then the evolutionary trends evident in the *I. vireti*-*I. atticus* lineage are likely to have been continued in the hypothetical *Indarctos*-*Agriotherium* lineage. This is, indeed, the case, and Crusafont & Kurtén's comments quoted above apply equally well to *Agriotherium* relative to *I. atticus*. Such general trends do not necessarily constitute proof of a direct phylogenetic relationship between the two taxa.

Much more convincing evidence comes from an examination of certain tooth and skull characters in advanced *Indarctos* (i.e. those between 6 and 9 m.y. old), and early *Agriotherium* (i.e. those that are, or probably are, about 5 m.y. old). Examples of the latter are *A. africanum* from Langebaanweg, *A. insigne* from Europe (Montpellier), and *A. palaeindicum* from the Siwaliks. Advanced *Indarctos* includes *I. atticus* from Europe (Samos) and Iran (Maragha), *I. punjabiensis* from the Siwaliks, and North American *Indarctos*. All recorded specimens of the latter are here referred to the species *I. oregonensis* (see p. 101).

The classification of material referred to some of the above species has long been complicated by specimens which exhibit a combination of characters 'typical' of both genera. Pilgrim (1932: 44-46) discussed such a problem involving three incomplete mandibles from the Dhok Pathan of the Siwaliks (GSI-D8, D9, D10), and although he found it 'difficult to give a definite answer', he decided to reverse the identifications suggested by Lydekker (1884). Pilgrim's identifications are accepted here, with D8 assigned to *Agriotherium palaeindicum*, while D9 and D10 are assigned to *Indarctos punjabiensis*. The latter has since been recognized as one of the more advanced representatives of *Indarctos* (Thenius 1959), while *A. palaeindicum* is one of the more primitive representatives of *Agriotherium* (Hendey 1977).

It is highly likely that more will yet be written on the identity of the Siwaliks' *Indarctos* and *Agriotherium*. Both Pilgrim and Lydekker may have been incorrect in their interpretation of GSI-D8, D9 and D10 (and other specimens) since they could represent a single species which was no more variable than the Langebaanweg *Agriotherium*. The anomalous situation in respect of *I. punjabiensis* and *A. palaeindicum* will be repeatedly evident in the discussions which follow. The study of new and well provenanced material from the Siwaliks may resolve a situation which is beyond satisfactory resolution on the basis of available evidence.

Whatever the final outcome of this controversy, the fact that specimens can with some justification be identified with either *Indarctos* or *Agriotherium* is here regarded as highly significant, with specimens such as GSI-D8, D9 and D10 being interpreted as 'intermediates' between 'typical' *Indarctos* and 'typical' *Agriotherium*. The present study has shown that such 'intermediates' are more common than has hitherto been supposed. The characters which the two genera have in common, coupled with apparent evolutionary trends linking them, provide surprisingly good evidence for the transition of *Indarctos* to *Agriotherium* considering the relatively poor fossil record of the taxa concerned.

Indarctos-Agriotherium 'intermediates' are included in the *A. africanum* assemblage, while an undescribed *A. insigne* specimen from Montpellier (NMB-MP549) and the recently described *Indarctos* skull from Florida (Wolff 1978) are also in this category. The Florida skull is perhaps the best single recorded specimen which is 'intermediate' between 'typical' *Indarctos* and 'typical' *Agriotherium*. The age of this specimen is 'late Hemphillian' (Wolff 1978: 1), and it probably dates back about 6 m.y. It is certainly younger than the Samos *I. atticus* skulls described by Helbing (1932) and Thenius (1949, 1959), and it is much younger than the skull of *I. vireti* from Spain (Crusafont & Kurtén 1976). On the other hand, it is probably a little older than the skull of the Langebaanweg *A. africanum*.

Judging from the few measurements given by Wolff (1978), and from illustrations, the Florida skull is appreciably larger than that of *I. atticus*, which in turn is larger than that of *I. vireti* (Crusafont & Kurtén 1976). The trend of increasing size with time in the *Indarctos* lineage is clearly illustrated by these specimens. This trend was continued with the evolution of *Agriotherium*, since the skull of *A. africanum* is, in some respects at least, still larger than that of the Florida *Indarctos*. In respect of size the Florida skull is probably closer to that of *A. africanum* (and *A. sivalense*) than the three described skulls of European *Indarctos*.

The general similarity between the skulls of the Florida *Indarctos* and *A. africanum* was discussed earlier (see pp. 9-16), while the differences between them can all be ascribed to the more advanced condition of the latter. The advances are probably all related to the larger size of the *A. africanum* skull, and to modifications of its masticatory apparatus.

Judging from the Florida *Indarctos* and *A. africanum* skulls, the following are the most significant cranial characters shared by advanced *Indarctos* and *Agriotherium*:

1. Snouts relatively short and broad.
2. Zygomatic arches very stout and of similar shape.
3. Sagittal crest very high.
4. Overall similarity of the basicranial regions, particularly the absence of the alisphenoid canal, and the positions of the oval, postglenoid and other foramina.

In respect of the development of the snout, zygomatic arches and sagittal crests, the Florida *Indarctos* is intermediate between *I. atticus* and *A. africanum*. The basicranial region of *I. atticus* is similar to those of the other two skulls, and, according to Crusafont & Kurtén (1976), the basicranial region of *I. vireti* is similar to that of *I. atticus*. *I. vireti* is more primitive, however, in having the 'facial part of the skull . . . relatively much longer than in *I. atticus*' (Crusafont & Kurtén 1976: 10).

The relatively short snout of *Agriotherium* goes together with a relatively short palate, which is of interest because Kurtén (1964: 22) found that the

palate of the polar bear, *Thalarchos*, is slightly shorter than that of the brown bear, *U. arctos*, a pattern which he was not 'able to match . . . in any other bear population'. Evidently the *Indarctos*-*Agriotherium* example was not taken into account, but it is a parallel to *U. arctos*-*Thalarchos* in this respect. Kurtén (1967) subsequently noted that, like *Thalarchos*, a short and broad snout characterizes *Arctodus*, another ursid which is convergent with *Agriotherium* (see p. 51).

Another apparent similarity between the skulls of *Agriotherium* and *Thalarchos* is that in lateral view they have a relatively straight profile, with the sagittal crest prominent (Erdbrink 1953). It was on this basis that Wagner (1837) proposed the name *Agriotherium* for the *Ursus sivalensis* of Falconer & Cautley (1836) (see Erdbrink 1953: 557). *Thalarchos* is like *Agriotherium* and *Arctodus* in being a carnivorous animal descended from an omnivorous ancestor, and other parallels between them will be mentioned below.

The presence of a premaseteric fossa in the mandible of *Agriotherium*, and its absence in *Indarctos*, is an important distinguishing characteristic, the significance of which has prompted much published and unpublished comment. In one recent account it was erroneously stated that the premaseteric fossa is also characteristic of *Ursavus* (Hendey 1977), an error stemming from Frick (1926: 99), citing Wegner (1913). In fact, *Ursavus*, like *Indarctos*, lacks this fossa, and it is thus peculiar to *Agriotherium* in the hypothetical *Ursavus*-*Indarctos*-*Agriotherium* lineage.

The premaseteric fossa is important from a phylogenetic point of view, since it, like other 'characteristics', may not be an invariably diagnostic feature of *Agriotherium*. For example, it is absent from at least one mandible which has been assigned to *Agriotherium*, namely, the *A. palaeindicum* specimen GSI-D8. On the other hand, in the Samos *I. atticus* specimen described by Thenius (1959) (NMW-Samos 1912, 29), there is a slight depression in the premaseteric region which could be an incipient fossa. No such fossa, however, has been reported in more advanced *Indarctos*, such as that from North America.

Thenius (1959) pointed out that most of the *Indarctos* mandibles then known were either incomplete or belonged to immature individuals, and that the premaseteric fossa was either not observable or absent. This fossa clearly is an ontogenetic character, since in the Langebaanweg assemblage it is well developed only in older individuals (e.g. L45062), and is shallow in the mandible of a young adult (L45114) (Fig. 33).

A premaseteric fossa is otherwise known amongst ursids in Hemicyoninae and Tremarctinae. Although the early history of tremarctines is not well known (Thenius 1976), there is nothing to indicate that they and the hemicyonines are closely related. Consequently, it is certain that the premaseteric fossa in these two groups was evolved independently. There is thus no reason to suppose that its presence in *Agriotherium* is indicative of a close relationship with either the Hemicyoninae or the Tremarctinae. Since the significance of the premaseteric fossa in ursids is not known (Davis 1955), there is no way of knowing why it should develop in some lineages and not in others.

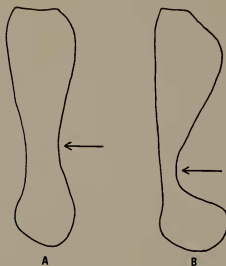


Fig. 33. Dorsoventral cross-sections of Langebaanweg *Agriotherium* hemimandibles with arrows indicating premasseteric fossae. A. L45114. B. L45062.

The teeth of *Indarctos* and *Agriotherium* provide much evidence in support of the theory that they are directly related.

As is often the case with carnivore incisors and canines, little of significance emerged from a study of these teeth in *Indarctos* and *Agriotherium*, except that they are essentially similar morphologically. The I^1 and I^2 are perhaps the most distinctive of the anterior teeth in *A. africanum*, and they are closely matched by those of the *I. atticus* specimen from Samos described by Helbing (1932, fig. 2) (NMB-Sam31). The anterior teeth of *Agriotherium* are distinguished from those of *Indarctos* principally by their larger size, this being a reflection of the overall size differences between the two genera.

It is worth noting in this connection that since the *Agriotheriinae*, like other ursids, exhibit appreciable sexual dimorphism, it is possible that large males of advanced *Indarctos* were of similar size to, and perhaps even slightly larger than, small *Agriotherium* females. For example, in terms of overall size the maxillary fragment of a small *A. insigne* specimen from Montpellier (NMB-MP549) is virtually identical in size to corresponding parts of the Vienna *I. atticus* specimen (NMW-Samos 1912, 29) (Fig. 34). Similarly, the Florida *Indarctos* skull is in some respects as large as that of the Langebaanweg *Agriotherium*, which belongs to a male, and would therefore have been larger than those of *A. africanum* females. Thus size alone may not necessarily be a reliable criterion for distinguishing the two genera.

One of the general trends in ursid evolution has been the emphasis on the development of the posterior cheek teeth, and the reduction in size or even loss of the anterior premolars (P_1^1 - P_3^3). More reduced premolars is one of the charac-

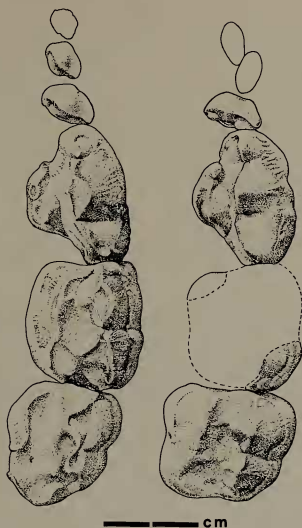


Fig. 34. Upper cheek tooth rows of *Indarctos atticus*, NMW-Sam1912/29 (left) and *Agriotherium insigne*, NMB-MP549 (right). Drawn from casts.

ters which distinguishes *I. atticus* from the earlier *I. vireti* (Crusafont & Kurtén 1976). In *I. atticus* P_1^1 and P_2^2 are apparently always single-rooted, while P_3^3 usually have two roots, although P_3 may sometimes have only one root (Thenius 1959). In the Florida *Indarctos* P_1 and P_2 are single-rooted, and P_3 is double-rooted (Wolff 1978).

Judged on the basis of the Langebaanweg sample, the anterior premolars of *Agriotherium* had undergone even further reduction, since in this instance all are invariably single-rooted and as many as two of a series may be lost (Table 16). This sample does not, however, exhibit one of the extremes in anterior premolar development encountered in *Agriotherium*. The Montpellier *A. insigne* specimen, NMB-MP549, is like advanced *Indarctos* in having a

TABLE 16
Anterior premolars in *Agriotherium* from Langebaanweg.

		P ¹	P ²	P ³	P ₁	P ₂	P ₃
L41404	. .	p	p	p	—	—	—
L50003	. .	—	—	—	p	p	p
L50445	. .	—	—	—	p	p	p
L40044	. .	—	—	—	p	a	p
L50004	. .	—	—	—	p	a	p
L50903	. .	—	—	—	p	a	p
L45062	left	p	a	p	p	a	p
	right	p	a	p	p	a	a
L45114	. .	—	—	—	a	a	p

p = present; a = absent.

double-rooted P³ set transversely in the jaw. It is especially reminiscent of the Vienna *I. atticus* specimen in this respect (Fig. 34), the only difference being that the principal cusp in the latter is slightly more distinct. The P³ of NMB-MP549 is unlike that of any other recorded *Agriotherium*.

By contrast, the Vienna *I. atticus* specimen is *Agriotherium*-like in having the P₁ to P₃ reduced to single-rooted teeth.

Thus, in respect of anterior premolar development conditions typical of advanced *Indarctos* may occasionally be found in *Agriotherium*, and vice versa. In addition, the anterior premolars of *Agriotherium* are morphologically similar to those of advanced *Indarctos*, except for the slightly more distinct principal cusps in the latter. This is a primitive characteristic since the principal cusps of the anterior premolars of *I. atticus* are in turn less well developed than those of *I. vireti*.

The P₄'s of advanced *Indarctos* and *Agriotherium* are also almost indistinguishable in terms of their basic morphology. Differences in detail are probably no greater than those in the Langebaanweg *Agriotherium* sample, which includes one specimen (L50445) with the principal cusp configuration resembling that in the *I. atticus* specimen, NMB-Sam31 (Fig. 35). Of particular significance is the tendency in *Indarctos* for the development of a postero-internal bulge in the circular region. This feature is well developed in the Maragha *I. atticus* specimen (De Mecquenem 1925). In *Agriotherium* the postero-internal bulge on P₄ is comparably developed, whereas it is absent or much less pronounced in all other ursids.

The principal differences between the P₄'s of advanced *Indarctos* and *Agriotherium* are that the latter are higher crowned and tend to be larger in

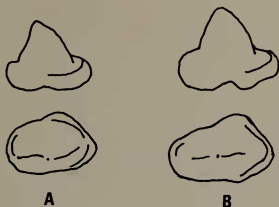


Fig. 35. Buccal and occlusal views of P_4 's.
A. *Indarctos atticus*, NMB-Sam31 (after Helbing 1932, fig. 3). B. Langebaanweg *Agriotherium*, L50445.

overall size. All the posterior cheek teeth of *Agriotherium* are higher crowned than their counterparts in *Indarctos*, although the Florida *Indarctos* specimen may be an exception in this respect. Apparently the crown height increase in the *Indarctos*-*Agriotherium* lineage was more or less in proportion to the overall increase in the size of the taxa concerned.

A likely parallel of this situation is that involving *Thalarchos*, which has relatively higher crowned posterior cheek teeth than *Ursus arctos* (Kurtén 1964).

In the case of the upper carnassial (P_4), it is the nature of the protocone lobe and the development of the parastyle which are of particular phylogenetic significance.

As a general rule the P_4 of *Agriotherium* is distinguished from that of *Indarctos* by the presence of a parastyle. However, some specimens of *Indarctos* do have a P_4 parastyle, although it is usually less prominent than that of *Agriotherium*. For example, this cusp is present in *I. atticus* from Conclud (Crusafont & Kurtén 1976) and Samos (Helbing 1932; Thenius 1959), *I. punjabiensis* from the Siwaliks (Lydekker 1884), and North American *Indarctos* (Merriam *et al.* 1925; Merriam & Stock 1925; Wolff 1978). The parastyle is particularly well developed in some North American specimens (e.g. the Florida skull), which are younger than European *I. atticus*. This cusp is absent in the still older and more primitive *I. arctoides* and *I. vireti*. There was thus a tendency for the development of a P_4 parastyle in the *Indarctos* lineage, and this was continued in the presumed descendant, *Agriotherium*, in which this cusp is always present and well developed.

As far as is known the only other ursids in which the P_4 parastyle is present are *Ursavus depereti* and its possible descendant, the giant panda, *Ailuropoda melanoleuca* (see p. 96).

The situation in respect of the P_4 protocone lobe is slightly different, although equally informative. According the Crusafont & Kurtén (1976: 8)

there was a tendency for *I. vireti* to develop an antero-internal cusp on the P^4 , a situation which 'is not uncommon in *I. arctoides* and *I. atticus*'. This cusp is also present in the *I. punjabiensis* specimen, GSI-D6, although in this instance it is rather small (Lydekker 1884). In the younger and more advanced North American *Indarctos* this cusp is either reduced (Wolff 1978) or absent (Merriam & Stock 1925). This indicates that while a double-cusped protocone lobe is characteristic of most *Indarctos*, there was a tendency for the antero-internal cusp to be reduced or lost in advanced forms.

By contrast, an antero-internal cusp is found only in some of the earlier Old World representatives of *Agriotherium*, namely, *I. insigne* from Montpelier (NMB-MP549) and the Langebaanweg *A. africanum*. In the case of the latter, this cusp is best developed in the holotype, L2045, from bed 3aS, which predates those *A. africanum* P^4 's from bed 3aN in which the antero-internal cusp is small or absent.

Indications are, therefore, that early forms of European and African *Agriotherium* still had an antero-internal cusp on P^4 , but this was soon reduced and lost. On the other hand, no Asian or North American *Agriotherium* is known to have had this cusp, which had already been reduced and lost in the advanced *Indarctos* of these continents. This suggests that the *Indarctos*-*Agriotherium* lineage may have had at least two geographically separated branches, one in Europe and Africa and the other in Asia and North America, which in respect of their P^4 protocone lobes evolved at different rates. The implications of this possibility will be discussed later (see pp. 101-4).

Reduction of the P^4 protocone is a characteristic of the *Ursus*-*Thalarctos* lineage (Kurtén 1964), and in South American *Arctodus* (Kurtén 1967). This is another example of a parallel development in *Agriotherium*, *Thalarctos* and *Arctodus*.

Once again a double-cusped protocone lobe is otherwise known only in *Ursavus depereti* and *Ailuropoda*, although in these taxa the morphology of the lobe is somewhat different (see p. 96).

As with the upper carnassial, the lower one (M_1) is an important tooth in indicating the origins of *Agriotherium*. There is, however, a complication with M_1 , although in the final analysis its phylogenetic significance is not diminished. The complication concerns the identification of the posterolingual cusps of this tooth.

The cusp of the *Agriotherium* M_1 which has invariably been identified as the metaconid may in reality be the entoconid. If this is, indeed, the case, then the metaconid of the *Agriotherium* M_1 is either reduced or absent, usually the latter.

Both the metaconid and entoconid are present and well developed in *Ursavus* and *Indarctos*, although with time the metaconid becomes a progressively less prominent feature of M_1 , since it is reduced in size relative to the entoconid and is increasingly overshadowed by the protoconid. In *U. primaevus* the metaconid is larger and more prominent than the entoconid, and is only

slightly less high-crowned than the protoconid (e.g. Crusafont & Kurtén 1976, fig. 13). Much the same applies in the case of *I. vireti* and *I. arctoides*, except that in these species the metaconid and entoconid are of comparable size (Crusafont & Kurtén 1976, fig. 2; Tobien 1955, fig. 3). In *I. atticus* the metaconid is much less prominent than the protoconid, but is still of similar size to the entoconid (Helbing 1932, fig. 3).

In the smallest of the *A. africanum* M₁'s (L50006) what is interpreted as a vestigial metaconid is still present. It is completely overshadowed by the protoconid, and, unlike its counterpart in *I. atticus*, is smaller than the entoconid. The metaconid is absent in all other M₁'s from Langebaanweg, and, apparently also from all other recorded *Agriotherium* M₁'s. The progressive reduction and eventual loss of the M₁ metaconid in the *Ursavus-Indarctos-Agriotherium* lineage is illustrated in Figure 36.

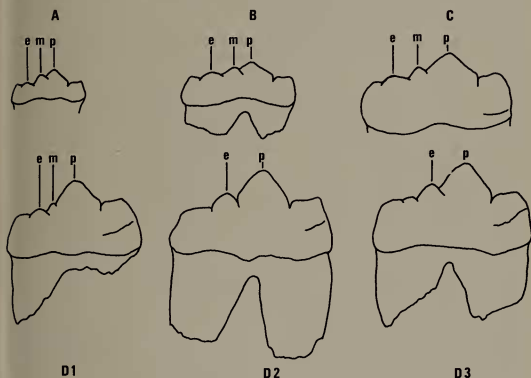


Fig. 36. M₁'s. A. *Ursavus primaevus* (after Crusafont & Kurtén 1976, fig. 14). B. *Indarctos arctoides* (after Tobien 1955, fig. 3). C. *Indarctos atticus* (after Helbing 1932, fig. 3). D. Langebaanweg *Agriotherium* (D1—L50006; D2—L50004; D3—L50446). All are lingual views except C, which is a buccal view with the buccal talonid cusps omitted. e—entoconid; m—metaconid; p—protoconid.

If the largest of the posterolingual M₁ cusps in *Agriotherium* is indeed the entoconid (i.e. a talonid cusp), rather than the metaconid (i.e. a trigonid cusp), this would account for Tobien's (1955: 14) observation that the 'Metaconid' of *Agriotherium* is 'niedriger und starker zurückgeschoben', while in *Indarctos* it is

'höher und näher an das Protoconid gestellt'. The cusp which Tobien believed to be the metaconid in *Agriotherium* may simply be a well-developed entoconid in more or less its usual position, while in *Indarctos* the metaconid was correctly identified as such, and it, too, is in its usual position.

The metaconid in *Indarctos* has a counterpart on the buccal side of the talonid, this being a small cusp situated between the protoconid and hypoconid. It is present in *I. vireti* (Crusafont & Kurtén 1976), *I. atticus* (Helbing 1932), *I. oregonensis* (Dalquest 1969), and other specimens, although traces of its presence may be obliterated by wear. A vestige of this cusp may be represented in the *A. palaeindicum* specimen, GSI-D8, by a slightly inclined ridge anterior to the hypoconid. A similar ridge is present in the M_1 of *A. africanum*, although in this species it takes the form of an undemarcated horizontal extension of the hypoconid. It meets with the posterobuccally directed keel of the protoconid. L50006 is also unusual in lacking this keel and in having the hypoconid ridge linked directly with the vestigial metaconid.

The reduction and loss of the M_1 metaconid in the *Indarctos*-*Agriotherium* lineage thus appears to have been accompanied by reduction and loss of its buccal counterpart. The impression gained is that these cusps were 'absorbed' by the protoconid, which is considerably enlarged in *Agriotherium*. This is a manifestation of the development of the shearing cusps (paraconid and protoconid) at the expense of the crushing cusps (talonid cusps) in the *Indarctos*-*Agriotherium* lineage.

It is possible, however, that the traditional interpretation of the large posterolingual M_1 cusp in *Agriotherium* as the metaconid is correct. Another of the Langebaanweg specimens, L50446, is unusual in having the largest of the posterolingual cusps flanked posteriorly by two smaller cusps, whereas in all other specimens there is only one such cusp. An almost exact match of L50446 is the M_1 of the *A. palaeindicum* specimen, GSI-D8 (Lydekker 1884). If the largest of the posterolingual cusps in these specimens are metaconids, then the smaller cusps immediately posteriorly would be the entoconids. It would, therefore, be the entoconid which is lost in other *Agriotherium* M_1 's, and this, rather than the loss of the metaconid, would have characterized the *Indarctos*-*Agriotherium* lineage. This hypothetical link would then be supported by the observation that the entoconid is as well developed in *Agriotherium* specimens such as L50446 and GSI-D8 as it is in some advanced *Indarctos* (e.g. *I. oregonensis*—Dalquest 1969, fig. 4).

In the case of the first alternative suggested above, the two smaller posterolingual cusps in L50446 and GSI-D8 would be interpreted as a duplication of the single cusp in this position in other *Agriotherium* M_1 's.

A first-hand examination of all relevant specimens may be necessary before deciding which of the above alternatives is likely to be correct. Irrespective of which applies, a transition from the typical *Indarctos* condition to that typical of *Agriotherium* is documented by specimens from the Siwaliks and Langebaanweg.

Another trend evident in the lower carnassials of *Indarctos* and *Agriotherium* is that of a reduction in their relative lengths with time (Table 17). Only the problematical Siwaliks' specimens GSI-D8 and D9 are anomalous in terms of their length: breadth ratios.

The arrangement and morphology of the M^1 cusps in advanced *Indarctos* and *Agriotherium* is virtually identical. The M^1 of *A. africanum* differs from that of *I. atticus* only in being relatively shorter and higher crowned, although it may be indistinguishable from more advanced *Indarctos* (e.g. the Florida specimen) in these respects.

In most, and perhaps all, *Indarctos* M^1 's the posterior keels of the metacone and hypocone are linked across the posterior end of the tooth by a low ridge of enamel. This feature is present but less obvious in *A. africanum*, and probably all other *Agriotherium*, and this region of the tooth also differs in being noticeably shorter than in the corresponding part of the *I. atticus* M^1 . In other words, there is a very short 'talon' region in the latter, and it is reduction of this feature which contributes to the overall shortening of M^1 in *Agriotherium*.

TABLE 17

Length : breadth ratios of *Indarctos* and *Agriotherium* M^1 's.

TAXON	LOCALITY and/or NUMBER	LENGTH	BREADTH	L : B	MEANS
<i>Agriotherium africanum</i>	{ L45062 L45062 L50004 L50006 L50446 L45114 L50005	39,7 39,7 43,4 37,8 44,0 43,1 43,9	23,0 22,3 24,8 21,1 23,4 22,8 22,9	1,73 : 1 1,79 : 1 1,75 : 1 1,79 : 1 1,88 : 1 1,89 : 1 1,92 : 1	1,82 : 1
<i>Agriotherium insigne</i>	Montpellier ¹ Montpellier ¹	40,0 38,0	22,5 21,5	1,78 : 1 1,79 : 1	1,79 : 1
<i>Agriotherium palaeindicum</i>	GSI-D8 ²	42,7	21,3	2,00 : 1	2,00 : 1
<i>Indarctos punjabiensis</i>	GSI-D9 ²	39,6	21,1	1,88 : 1	1,88 : 1
<i>Indarctos atticus</i>	NMB-Sam31 NMW-Sam1912/29 ³ Concud ⁴	41,6 39,3 42,4	22,2 20,4 22,2	1,87 : 1 1,93 : 1 1,91 : 1	1,90 : 1
<i>Indarctos arctoides</i> ⁴	Westhofen Pfaffstetten Montredon	32,6 30,8 35,7	17,3 15,8 18,3	1,88 : 1 1,95 : 1 1,95 : 1	1,93 : 1
<i>Indarctos vireti</i> ⁴	Can Llobateres VP633 { VP647 VP647 Can Purull Type (<i>pontiensis</i>) Type	32,7 30,2 30,0 c. 34,5 30,8	16,8 14,9 14,7 17,3 15,1	1,95 : 1 2,03 : 1 2,04 : 1 1,99 : 1 2,04 : 1	2,01 : 1

¹ Viret 1939; ² Lydekker 1884; ³ Thenius 1959; ⁴ Crusafont & Kurtén 1976.

This is a significant difference, because once again a specimen of one genus is known which has the character of the other. An *Indarctos*-like post-metacone lengthening is one of the few features visible on the incomplete and badly restored M^1 of the Montpellier *A. insigne* specimen, NMB-MP549.

The 'primitive' M^1 of this remarkable specimen is yet another of its *Indarctos* 'characteristics', others being its relatively small size, double-rooted and transversely orientated P^3 , and double-cusped P^4 protocone lobe. This specimen also has the P^4 , M^1 and M^2 lower crowned than any of their counterparts in the Langebaanweg assemblage. However, it is identified with *Agriotherium* because its M^2 is of the *Agriotherium* type and distinct from that of all specimens referred to *Indarctos* (see below). Had the M^2 of this specimen not been preserved, it may well have been referred to *Indarctos*. Montpellier could therefore have erroneously acquired the distinction of being the only locality where *Indarctos* and *Agriotherium* occurred together. This imaginary situation is mentioned here to indicate the importance of NMB-MP549 as an *Indarctos*-*Agriotherium* 'intermediate', and to illustrate how easy it is to misidentify specimens belonging to late *Indarctos* and early *Agriotherium*. The possibility of similar confusion with certain Siwaliks specimens was mentioned above.

Before dealing with the next tooth in the dentition, another parallel between *Agriotherium* and *Thalarctos* is mentioned. The M^1 of the latter is relatively shorter and higher crowned than that of *U. arctos*, its 'structural' ancestor (Kurtén 1964). This also applies in the case of at least some species of *Arctodus* (Kurtén 1967).

The M_2 of *A. africanum*, and other *Agriotherium*, usually consists of two trigonid cusps side by side, flanked posteriorly by two similarly positioned talonid cusps. The M_2 of *Indarctos* differs only in having two lingual talonid cusps, and in being relatively longer and narrower. There are, however, *Agriotherium* specimens which are *Indarctos*-like in both these respects. The M_2 of the *A. palaeindicum* specimen GSI-D8 has two lingual talonid cusps, while vestiges of a second cusp are visible in the Langebaanweg specimens L54114/L46563 and L50007. The length:breadth ratios of the M_2 's of GSI-D8 and L45114/L46563 are comparable to those of *I. atticus* M_2 's (Table 18). By contrast, this ratio in the *I. punjabiensis* specimen GSI-D9 is the same as that of the mean of the *A. africanum* sample.

Curiously, the *A. africanum* M_2 's which are most *Indarctos*-like in respect of talonid cusps and proportions are those which are most specialized in terms of their trigonid development (see p. 27). Consequently, these specimens should not be considered as good *Indarctos*-*Agriotherium* intermediates. In addition, it could be argued that Pilgrim (1932) was incorrect in reversing Lydekker's (1884) identifications of GSI-D8 and D9 and that they, too, are not 'intermediates' in the sense claimed above. This may, indeed, be the case, but the fact remains that however these (and other) Siwaliks specimens are identified, they exhibit a combination of *Indarctos* and *Agriotherium* characters.

The dentitions of *Indarctos* and *Agriotherium* are perhaps most clearly

TABLE 18

Length : breadth ratios of *Indarctos* and *Agriotherium* M₂'s.

TAXON	LOCALITY and/or NUMBER	LENGTH	BREADTH	L : B	MEANS
<i>Agriotherium africanum</i> .	{ L45062 L45062 L50004 L50003 L50007 L45114 L46563	28,6 29,3 32,3 30,4 28,8 32,6 34,0	c. 23,6 24,0 26,0 24,1 21,9 23,5 24,3	1,21 : 1 1,22 : 1 1,24 : 1 1,26 : 1 1,32 : 1 1,39 : 1 1,40 : 1	1,29 : 1
<i>Agriotherium insigne</i> .	Montpellier ¹	30,2	23,2	1,30 : 1	1,30 : 1
<i>Agriotherium palaeindicum</i> . .	GSI-D8 ²	31,8	22,9	1,39 : 1	1,39 : 1
<i>Indarctos punjabiensis</i> .	GSI-D9 ³	29,2	22,6	1,29 : 1	1,29 : 1
<i>Indarctos atticus</i> . .	NMB-Sam31 NMW-Sam1912/29 ³	32,4 28,7	23,3 20,8	1,39 : 1 1,38 : 1	1,39 : 1
<i>Indarctos arctoides</i> ⁴ .	Montredon Westhofen Pfaffstetten	25,2 25,2 24,1	19,0 17,4 16,5	1,33 : 1 1,45 : 1 1,46 : 1	1,41 : 1
<i>Indarctos vireti</i> ⁴ . .	Can Llobateres VP633 VP640/1 { VP647 VP647 Can Purull Type Type (<i>pontiensis</i>)	25,0 26,1 23,7 23,6 22,0 25,6	17,2 18,0 16,2 16,2 15,6 17,7	1,45 : 1 1,45 : 1 1,46 : 1 1,46 : 1 1,41 : 1 1,45 : 1	1,45 : 1

¹ Viret 1939; ² Lydekker 1884; ³ Thenius 1959; ⁴ Crusafont & Kurtén 1976.

distinguished from one another by the fact that the M² of the latter lacks a talon, whereas in *Indarctos* this feature, although variably developed, is always present.

The postero-internal (talon) region of the *Agriotherium* M² is also variably developed, the Langebaanweg assemblage being useful in indicating the variation possible in a single population (Fig. 12). Of particular interest is the isolated M², L47698, in which there is a marked posterior projection of the postero-internal part of the tooth. This is here interpreted as the vestiges of the talon characteristically present in the M² of *Indarctos*. L47698 is remarkably similar to the M², GSI-D12, referred to *I. punjabiensis* by Lydekker (1884, fig. 6), and these two specimens represent an intermediate between the conditions typical of *Indarctos* and *Agriotherium*. The progressive shortening and broadening of M²'s in the *Indarctos*-*Agriotherium* lineage is indicated by the data in Table 19.

Erdbrink's (1953: 582) view that there is 'at best a beginning of a [M²] talon . . . in *A. insignis*' is here regarded as the reverse of the true situation. *A. insigne*, like *A. africanum*, sometimes has the vestiges of a M² talon.

As with M¹, the arrangement and morphology of the four principal cusps of M² in advanced *Indarctos* and *Agriotherium* are very similar. The paracones

TABLE 19

Length : breadth ratios of *Indarctos* and *Agriotherium* M²s.

TAXON	LOCALITY OF NUMBER	LENGTH	BREADTH	L : B	MEANS
<i>Agriotherium africanum</i>	L48577	25,4	30,2	0,84 : 1	0,91 : 1
	L48564	25,6	30,5	0,84 : 1	
	L41404	26,5	31,0	0,85 : 1	
	{ L45062	26,5	30,2	0,87 : 1	
	{ L45062	26,4	29,9	0,88 : 1	
	{ L45137	29,3	31,5	0,93 : 1	
	{ L45137	29,5	31,4	0,94 : 1	
	L47242	25,8	25,9	1,00 : 1	
	L47698	31,1	30,1	1,03 : 1	
<i>Agriotherium insigne</i>	NMB-MP549	25,2	28,3	0,89 : 1	0,96 : 1
	Type ¹	27,4	26,5	1,03 : 1	
<i>Indarctos punjabiensis</i>	GSI-D12 ²	28,2	26,7	1,06 : 1	1,06 : 1
<i>Indarctos atticus</i>	NMW-Sam1912/29 ³	30,0	26,5	1,13 : 1	1,21 : 1
	NMB-Sam31	33,4	26,1	1,28 : 1	
<i>Indarctos arctoides</i>	Montredon ⁴	31,0	24,0	1,29 : 1	1,34 : 1
	Montredon ⁴	29,3	20,5	1,43 : 1	
	Orignac ⁴	28,2	22,0	1,28 : 1	
	Gau-Weinheim ⁵	25,1	18,3	1,37 : 1	
<i>Indarctos vireti</i>	VP633 ⁴	27,9	19,0	1,47 : 1	1,43 : 1
	VP646 ⁴	27,3	19,7	1,39 : 1	

¹ Frick 1926; ² Lydekker 1884; ³ Thenius 1959; ⁴ Crusafont & Kurtén 1976; ⁵ Tobien 1955.

and metacones are conical, with distinct anterior and posterior keels, the protocone is ridge-like, and, with the small hypocone, is lower than the buccal cusps.

The M²s of *Indarctos* and *Agriotherium* illustrate very clearly a progressive development from *I. vireti*, through *I. arctoides*, *I. atticus*, *I. punjabiensis* to *Agriotherium*, with *A. africanum* taken as an example of its genus (Fig. 37). The recorded M²s of advanced North American *Indarctos* all have well-developed talons, that of the *I. cf. oregonensis* specimen recorded by Merriam & Stock (1925) being the most prominent. It is, however, from the same deposits as another *I. oregonensis* M², which is a larger tooth but with a relatively smaller talon (Merriam *et al.* 1925). The latter is here interpreted as belonging to a male, while the smaller specimen with the larger talon belongs to a female.

This raises the possibility that the teeth of female *Indarctos* and *Agriotherium* tend to be more 'primitive' than those of the larger males. This explanation applies in the case of the 'primitive' *A. insigne* specimen, NMB-MP549, discussed earlier, which represents a small individual, apparently a female. Another example is the *A. africanum* M₁ with the vestigial metaconid, L50006. The female *I. cf. oregonensis* is also 'primitive' compared with other North American *Indarctos* in having a relatively small P⁴ parastyle and a relatively elongated M¹. It does not, however, have a double-cusped P⁴ protocone lobe. This, together with the fact that NMB-MP549 does not have a talon on M²,

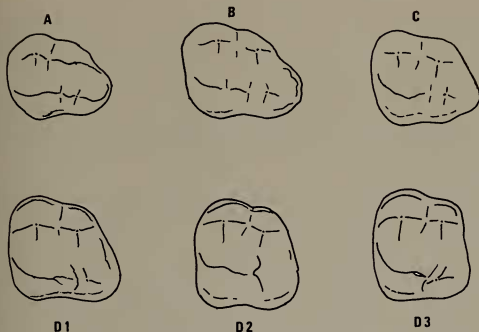


Fig. 37. M²s. A. *Indarctos arctoides* (after Helbing 1932, fig. 7). B. *Indarctos atticus* (after Helbing 1932, fig. 1). C. *Indarctos punjabiensis* (after Lydekker 1884, fig. 6). D. Langebaanweg *Agriotherium* (D1—L47698; D2—L45137; D3—L41404).

indicates that females were not necessarily 'primitive' in all respects. Nevertheless, since increasing size was a characteristic of the *Indarctos*-*Agriotherium* lineage, and consequently large size was itself an 'advanced' character, it is to be expected that larger individuals would also be 'advanced' in other respects, and vice versa. This is a further indication that allowance must be made for appreciable variation in characters in studies on *Indarctos* and *Agriotherium*. The fact that known North American *Indarctos* M²s appear more 'primitive' than the *I. punjabiensis* specimen, GSI-D12, does not necessarily mean that they must be older.

There is other evidence to support this opinion. Once again there is a parallel between *Agriotherium* and *Thalarcos*, since the latter also has the M² talon reduced, and it may sometimes even be absent. The study by Kurtén (1964) has shown that there is considerable variation in *Thalarcos* in this respect even within a single population. Particularly remarkable is a specimen in which the right M² talon is reduced, while that of the left M² is completely absent (Kurtén 1964: 17, pl. 4A). Such examples are exceptional, but presumably if samples of *Indarctos* as large as Kurtén's *Thalarcos* sample ($n = 113$) were available, similar specimens may be found. This suggests that undue reliance may have been placed on the value of the M² talon as a distinguishing characteristic of *Indarctos*.

The M₃ of *Indarctos* and *Agriotherium* is less commonly represented than other posterior cheek teeth, evidently because it is single-rooted and easily

separated from the mandible. It is nevertheless clear that this tooth was reduced in length in the *Indarctos-Agriotherium* lineage to a degree comparable to that of M^2 . In *I. vireti* the M_3 is markedly elongated anteroposteriorly and has a pronounced posterior tapering (Crusafont & Kurtén 1976). The M_3 of *I. atticus* is similar, but is less elongated, while that of *Agriotherium* is usually only as long as it is broad. The latter, however, is still *Indarctos*-like in having a pronounced posterior tapering. The *A. africanum* M_3 , L50981, is very like those of the Vienna and Basel *I. atticus* specimens (Thenius 1959; Helbing 1932) in shape.

The reduction of M_3 is another development shared by *Agriotherium* and *Thalarcos*.

Although mention has been made of differences in proportions in certain of the posterior cheek teeth discussed above, this matter warrants more detailed attention, since these differences are directly related to changes in tooth morphology and are as significant from a phylogenetic point of view. In addition, metrical data have the advantage of being easily represented diagrammatically and can thus give a visual impression of certain evolutionary changes in the hypothetical *Ursavus-Indarctos-Agriotherium* lineage. Five Old World species were selected to represent successive stages in this lineage. They are *Ursavus primaevus*, *I. vireti*, *I. arctoides*, *I. atticus*, and *A. africanum*. Individual species do not necessarily represent the stock from which the next in the series was derived, but are simply structurally suited to such a role. The lengths and breadths of their posterior cheek teeth are plotted in Figures 38-40.

It is clear from these figures that *U. primaevus* is in an isolated position, whereas there are similarities between *I. vireti* and *I. arctoides* on the one hand,

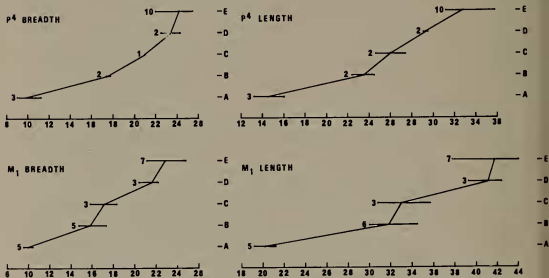


Fig. 38. Lengths and breadths of P^4 and M_1 . A. *Ursavus primaevus*. B. *Indarctos vireti*. C. *I. arctoides*. D. *I. atticus*. E. *Agriotherium africanum*. Sample sizes, ranges and means are indicated. Data from Crusafont & Kurtén (1976), Thenius (1959) and this report.

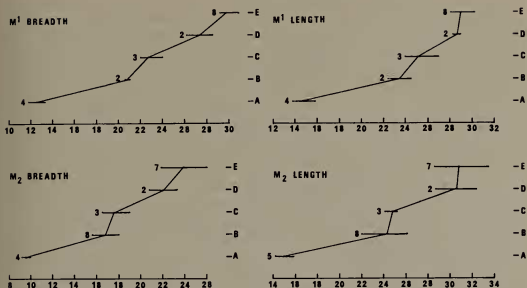


Fig. 39. Lengths and breadths of M^1 and M_2 of some Ursidae, (see Fig. 38 for key).

and *I. atticus* and *A. africanum* on the other. The isolated position of *U. primaevus* is not surprising since it is a contemporary of *I. vireti* (Crusafont & Kurtén 1976), and its phylogenetic connection with the *Indarctos-Agriotherium* lineage must be indirect. The fact that this lineage is divisible into two parts on the basis of cheek tooth size (and other evidence) is significant. The first is comprised of earlier, smaller and more primitive forms (i.e. *I. vireti*-*I. arctoides*), and the second of later, larger and more advanced forms (i.e. *I. atticus*-*A. africanum*).

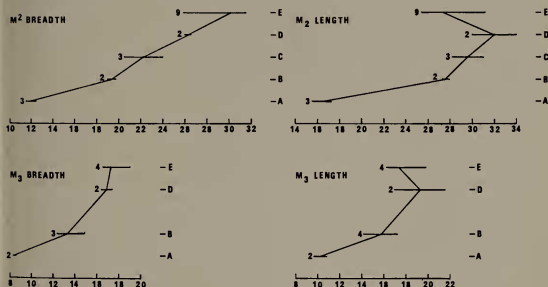


Fig. 40. Lengths and breadths of M^2 and M_3 of some Ursidae, (see Fig. 38 for key).

It is only in the last segment of the lineage that there are deviations from otherwise general trends in the lineage as a whole. The most obvious of these general trends was the increasing breadth of the posterior cheek teeth. This was probably more or less in proportion to the overall size increase of the taxa concerned. However, the situation in respect of the lengths of these teeth is more complex.

Only in the case of P^4 was there a tendency to increase length throughout the *Ursavus-Indarctos-Agriotherium* lineage. This is also a reflection of the increasing size of successive members of the lineage. In addition, it may be interpreted as indicating the increasing functional importance of the principal shearing tooth in the upper dentition, with the increased lengths of P^4 in the last stage of the lineage (i.e. *I. atticus-A. africanum*) being largely due to the development of the parastyle. It might be expected that there would have been a corresponding increase in the length of the lower carnassial. The fact that there is a barely perceptible increase in the mean length of the *A. africanum* M_1 over that of *I. atticus* may simply be due to the composite nature of this tooth, the increased length of the shearing element (i.e. the trigonid) being obscured by the reduction of the talonid.

By contrast, in the case of M^2 and M_3 the lengthening trend evident in most of the lineage is reversed in the *I. atticus-A. africanum* segment. This is a manifestation of the reduced importance of the crushing function of the most posterior cheek teeth in the last stage of the lineage.

The situation in respect of the lengths of the intermediate teeth, M^1 and M_2 , was itself intermediate, with lengths remaining static once the *I. atticus* stage was reached.

The overall impression gained from the study of the morphology and dimensions of the teeth of successive members of the *Ursavus-Indarctos-Agriotherium* lineage is that this lineage can be separated into two parts. Up to the *I. atticus* stage the taxa concerned were generalized 'omnivorous' ursids, but thereafter there were modifications of both tooth morphology and proportions being manifested which indicate adaptation to a more carnivorous diet. It may thus be more appropriate to think of 'advanced *Indarctos*' as being 'primitive *Agriotherium*'.

Since the transition from *Indarctos* to *Agriotherium* was gradual in the sense that there are specimens which exhibit 'characteristics' of both genera, it is far from obvious on what grounds the distinction between these genera is to be made. Earlier attempts to find distinguishing characters are now seen to have been inadequate. For example, lists of such characters given by Pilgrim (1932: 42) and Tobien (1955: 14) can be misleading and should be used with caution, if they are to be used at all. The formulation of mutually exclusive diagnoses for these genera has become difficult, if not impossible. There would, of course, be no problem if these diagnoses were to be based on a primitive *Indarctos*, such as *I. vireti*, and any of the species presently identified with *Agriotherium*. However, when all recorded intermediate forms are taken into

account, the diagnoses break down under a welter of qualifying statements. The situation could only become more confused if all the *Indarctos* and *Agriotherium* assemblages from the critical 5–8 Ma period were as large, or larger, than that from Langebaanweg. Even if this is never the case, the Langebaanweg assemblage has clearly shown that agriotheriines are as variable as other ursids, and consequently there can no longer be complacency about supposed 'characteristics' of individual representatives of this group.

This situation is here interpreted as indicating an ancestor–descendant relationship between *Indarctos* and *Agriotherium* beyond all reasonable doubt. In concluding his study of the Florida *Indarctos*, Wolff (1978: 11) stated that there are 'several cranial features [which] may indicate a relatively closer relationship between *Ailuropoda* and *Indarctos* than with other bears, although other possibilities exist'. In the light of the preceding discussion and the fact that the Florida *Indarctos* skull is even more like that of *A. africanum* than *Ailuropoda*, the 'other possibilities' must certainly include *Agriotherium*. The similarities between the skulls of advanced *Indarctos*, particularly the Florida specimen, and *Agriotherium* are so great that it is inconceivable that they are only distantly related. Wolff's concluding remarks refer specifically to 'great enlargement of the cheek teeth', 'expansions of the zygomatic arches and sagittal crests', and the 'absence of the alisphenoid canal' as shared characters indicative of the 'close relationship' between *Indarctos* and *Ailuropoda*. The fact that *Indarctos* and *Agriotherium* also share them is equally significant, especially taken in conjunction with all the other evidence cited above.

It seems superfluous at this stage to consider alternative theories on the origin of *Agriotherium*, but one is mentioned here since it apparently still has some support.

The fact that *Agriotherium* and the Hemicyoninae have a premasseteric fossa on the mandible in common has contributed to the belief that they are closely related (e.g. Frick 1926). There is also a superficial similarity between the dentitions of *Agriotherium* and hemicyonines, and both are supposedly canid-like, rather than ursine-like. This is indeed so in the case of hemicyonines, but in terms of the arrangement, morphology and size of individual cusps, the teeth of *Agriotherium* are far more like those of advanced *Indarctos* than any hemicyonine. It could, of course, be argued that the rather generalized hemicyonines are structurally suitable in both cranial and postcranial characters to be ancestral to *Agriotherium*. This more tenuous hypothesis is considered less likely than the alternative suggested here.

It was indicated earlier that the known temporal ranges of *Indarctos* and *Agriotherium* are in accord with the theory that the latter was derived from the former. In the case of the Hemicyoninae–*Agriotherium* alternative the situation is much less convincing because of an apparent, or actual, gap between the recorded histories of the taxa concerned.

In Europe *Agriotherium* is first recorded from the Ruscinian, whereas hemicyonines were extinct by the end of the Vindobonian (Table 20). This

TABLE 20

The occurrences of Hemicyoninae and *Agriotherium* in Europe.

TAXON	LOCALITY	MAMMAL AGE ¹	MEIN ZONE ²	APPROX. AGE IN m.y. ¹
<i>Agriotherium insigne</i>	Montpellier	Ruscinian	14	5
—	—	Turolian	11–13	—
—	—	Vallesian	9–10	—
<i>Hemicyon sansaniensis</i> , <i>Hemicyon goeriachensis</i> etc. ³	Wintershof-West, Sansan, Göriach, La Grive-St-Alban, Steinheim etc ³	Burdigalian to Vindobonian	3–8	13–18

¹ Van Couvering 1972, Fahlbusch 1976; ² Mein 1975, Fahlbusch 1976; ³ Heizmann 1973.

means that there was a period of about 8 m.y. for which no possible intermediate between hemicyonines and *Agriotherium* is known in Europe. Much the same applies in Asia and North America. It is unlikely that this could be due to a defective fossil record, since the period in question covers the Vallesian and Turolian (and their equivalents), of which the faunas are moderately to very well known. It is possible that the Hemicyoninae–*Agriotherium* transition took place in Africa, where 5–13 Ma faunas are poorly known, but negative evidence is hardly convincing support for a theory.

It is much more likely that the characters Hemicyoninae and *Agriotherium* have in common are due to convergent evolution. Parallel and convergent evolution often complicate studies of relationships, and the Ursidae are a group where this complication definitely exists. Early in the history of the Ursidae, the Amphicyoninae and Hemicyoninae evolved along parallel lines, while later the same applied to the Ursinae and Tremarctinae. *Agriotherium* is of particular interest in this connection, since not only is it intermediate in age between amphicyonines/hemicyonines and ursines/tremarctines, but it has in certain respects paralleled members of both sets of subfamilies.

The superficial similarities between *Agriotherium* and large amphicyonines and hemicyonines (e.g. *Amphicyon major*, *Dinocyon thenardi*) are striking enough to suggest that these animals were ecological vicars. On the other hand, *Agriotherium*, *A. major* and *D. thenardi* (and better known hemicyonines) also differ from one another in certain respects, which can be explained by their having evolved at different times from different ancestors.

Amongst the Ursinae, *Thalarcos* has now been mentioned several times as having evolved characters comparable to some in *Agriotherium*. In this instance there is no possibility of the shared characteristics being due to a close relationship. They are simply explained by the fact that both *Agriotherium* and *Thalarcos* are essentially carnivorous forms which evolved from omnivorous ancestors (Hendey 1972: 122). The relationship between *Thalarcos* and the *Ursus arctos* group has been well documented (Thenius 1953; Kurtén 1964),

and is here regarded as a parallel of the relationship between advanced *Indarctos* and *Agriotherium*. A more detailed search for parallelisms between these two sets of taxa may well be worth while. The obvious differences between *Agriotherium* and *Thalarcos* are not unexpected, since their ancestral forms are markedly different from one another. In addition, *Thalarcos* has as yet had a relatively brief history compared with that of *Agriotherium*. Given time it would no doubt become increasingly distinct from *U. arctos*, and perhaps become even more *Agriotherium*-like.

Agriotherium and advanced *Indarctos* are also paralleled in some respects by tremarctines, especially the large extinct species. For example, several references have been made above to similarities between the skull and skeleton of *A. africanum* and *Arctodus simus*. Merriam & Stock (1925: 5) found that there are certain characters 'in which *Tremarctos* and [*Arctodus*] show distinctly closer affinity to [*Agriotherium*] and its allies of the Pliocene than is seen in Pleistocene and Recent bears of the genus *Ursus*'. Others have thought this significant. For example, Erdbrink (1953) suggested that *Tremarctos* was closely related to the ursines, while the larger tremarctines were derived from advanced *Indarctos*. Kurtén (1966: 7) disagreed, and concluded that although the 'earlier history of *Arctodus* is poorly documented . . . there can be little doubt that it is a tremarctine, and not a member of the Agriotheriinae'.

The *Indarctos*-*Agriotherium* lineage was but one of several evolutionary developments amongst the Ursidae during the latter part of their history. As indicated above, it was a development which paralleled that undergone earlier by large amphicyonines and hemicyonines, but it, too, was ultimately unsuccessful and by the end of the Tertiary *Agriotherium* was on the verge of extinction, if not already extinct. It had no descendants.

Other later ursid lineages, however, were more successful. This applies particularly in the case of the one which gave rise to the Ursinae, which underwent a spectacular radiation beginning in the Pliocene. As with *Indarctos*-*Agriotherium*, the Ursinae also stemmed from *Ursavus*, and Thenius (1977 and earlier papers) has suggested *U. ehrenbergi* as the likely ancestral form.

The Tremarctinae were less successful than the Ursinae, having been confined to the Americas, and eventually being supplanted in North America by the Ursinae (Kurtén 1966, 1967). Their origins were recently considered by Thenius (1976), who suggested that they, too, stemmed from an *Ursavus*. Unfortunately, little is known of early tremarctines, but no doubt more will yet be learnt of the origins and early history of this group.

The origin of the giant panda, *Ailuropoda melanoleuca*, has long been a controversial issue. The earlier views that *Ailuropoda* is an ursid and not a procyonid, and that it had an agriotheriine ancestor (Hendey 1972), are maintained here, although it now appears that it may have stemmed from *Ursavus* and not *Indarctos* as previously suggested.

As indicated earlier, the skulls of *Ailuropoda* and advanced *Indarctos* have many characters in common which suggest that they are more closely related

to one another than to other bears. However, the latter had already undergone specializations in the direction of *Agriotherium* which render it structurally unsuitable as a stem form for *Ailuropoda*. For example, advanced *Indarctos* has reduced anterior premolars, while those of *Ailuropoda* are unusually large for an ursid. This objection does not apply in the case of earlier, unspecialized *Indarctos* (see Hendey 1972, table 1), but since such species have much in common with *Ursavus*, the latter must also be taken into account when considering the origin of *Ailuropoda*.

One of the less well-known species of *Ursavus* is *U. depereti* of the European Turolian, which is in some respects atypical of the genus (see Heizmann 1973). This applies particularly to the P⁴, and it is the unusual characteristics of this tooth which suggest that *U. depereti* may have a direct phylogenetic connection with *Ailuropoda*.

Casts of upper teeth of *U. depereti* from Soblay in France were recently examined in the Naturhistorisches Museum, Basel. The originals are in Lyon and were described by Viret (1949) and Viret & Mazenot (1949). Two P⁴'s are represented and they are remarkable for two reasons. Firstly, unlike the P⁴'s in other *Ursavus* species, the Soblay specimens have large parastyles. This cusp is proportionately even larger than those in advanced *Indarctos* and in *Agriotherium*, in which the parastyles are overshadowed by large and high-crowned paracones. The large parastyle and relatively low-crowned paracone of *U. depereti* are reminiscent of the situation in *Ailuropoda*, and differ from that in all other ursids. Secondly, the *U. depereti* P⁴ has an enlarged, double-cusped protocone lobe, which differs from that in *Indarctos* and *Agriotherium* in being more anteroposteriorly elongated and regular in occlusal outline. In addition, in the Soblay specimen, AA52 (Viret & Mazenot 1949, pl. 1 (fig. 6)), both cusps are ridge-like rather than pointed and are of more or less equal size. In all these respects the *U. depereti* P⁴ protocone lobe is *Ailuropoda*-like, and once again it differs from that in all other ursids.

The M¹ and M² of *U. depereti* are also basically similar in morphology to their counterparts in *Ailuropoda*. However, the upper molars are also similar to those of other *Ursavus* species and *Indarctos*, and are thus less significant in indicating a relationship with *Ailuropoda*. A possibly important characteristic of the M² figured by Viret & Mazenot (1949, pl. 1 (fig. 4)) is the rugose enamel of the occlusal surface, which could foreshadow the 'richly tuberculate' condition of the *Ailuropoda* M² (Davis 1964: 127).

The M₁ and M₂ of *U. depereti* also have the basic morphology characteristic of other *Ursavus* and *Indarctos*, although the M₁ is distinct, and more *Ailuropoda*-like, in having the metaconid more anteriorly situated (Schlosser 1902, pl. 2 (figs 20, 23)).

Slender though the evidence may be, *U. depereti* appears to be structurally better suited than any other recorded fossil ursid to fill the role of ancestor to *Ailuropoda*. In addition, it is also temporarily and geographically well suited to this role since it is from the continent on which the early evolution of living

bears was centred and it dates from a period when the radiation of later bears was just beginning. The absence of any intermediate forms may simply be due to the relatively poor Pliocene record in Asia, the continent to which *Ailuropoda melanoleuca* is confined (Chorn & Hoffmann 1978). Relevant fossils of Pliocene age, as well as better knowledge of *U. depereti*, are required to test this theory of *Ailuropoda* origins.

While the ultimate origins of both *Ailuropoda* and the *Indarctos*-*Agriotherium* lineage are uncertain, it is evident that these genera are more closely related to one another than to the Ursinae and Tremarctinae.

The radiation of the Ursidae, like that of some other mammalian families, was thus characterized by repetitious evolutionary developments, and the correct identification of relationships requires careful study of the fossil record. Ignorance of the details of this record may well lead to misinterpretation of the significance of similar, but independently evolved characteristics in ursid taxa. Kurtén (1967: 5) has found, for example, the analogy between European Miocene *Indarctos* and North American Pleistocene *Arctodus* to be 'truly astonishing and an example of the *déjà vu* experiences so familiar to the student of fossil bears'.

The relationships suggested here are indicated in Figure 41. The named late Tertiary species are all from Europe and consequently the European subdivisions of this period are used.

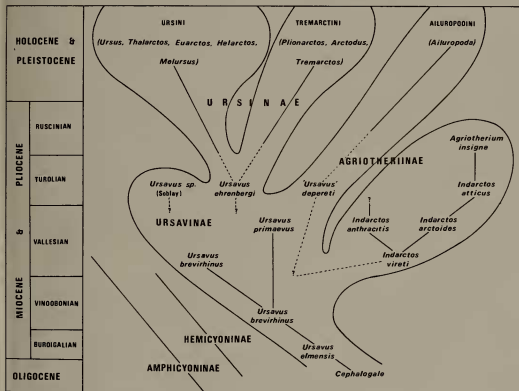


Fig. 41. Suggested relationships of some Ursidae.

NOMENCLATURE

The suprageneric classification of the Ursidae adopted here (Table 21) is a modification of an arrangement suggested earlier (Hendey 1972: 119), and is based on the phylogenetic relationships indicated in Figure 41.

TABLE 21
A classification of the Ursidae.

SUBFAMILY	TRIBE	GENERA, SPECIES
Amphicyoninae	Not subdivided	† <i>Amphicyon</i> , † <i>Cynelos</i> and †others
Hemicyoninae	Not subdivided	† <i>Hemicyon</i> , † <i>Dinocyon</i> and †others
Ursavinae	Not subdivided	† <i>Ursavus</i>
Agriotheriinae	Agriotheriini	† <i>Indarctos</i> , † <i>Agriotherium</i>
	Ailuropodini	† <i>'Ursavus' depereti</i> , <i>Ailuropoda</i>
Ursinae	Tremarctini	† <i>Plionarctos</i> , † <i>Arctodus</i> , <i>Tremarctos</i>
	Ursini	<i>Ursus</i> , <i>Thalarchos</i> , <i>Euarctos</i> , <i>Helarctos</i> , <i>Melursus</i>

† = extinct

In preceding sections of this report the generally accepted practice of allowing the ursines and tremarctines subfamilial status has been followed. With this as a precedent, it follows that the agriotheriines and *Ailuropoda* each warrant similar status. Some of those who have included *Ailuropoda* in the Ursidae have, indeed, placed it in a separate subfamily (e.g. Pilgrim 1932). Similarly, the agriotheriines have been widely recognized as a valid subfamily (e.g. Kurtén 1966).

A disadvantage with this arrangement is that it does not indicate the apparently close relationships between the ursines and tremarctines on the one hand (Kurtén 1966, 1967; Thenius 1976), and the agriotheriines and *Ailuropoda* on the other (Hendey 1972; Wolff 1978; this report). This problem is overcome by reducing the status of the four subfamilies to tribes, and then separating them into two subfamilies, namely, the Agriotheriinae (Agriotheriini and Ailuropodini) and the Ursinae (Ursini and Tremarctini). Except for the position of the Tremarctini, this was the arrangement suggested earlier (Hendey 1972), and for which there has been some support (e.g. Chorn & Hoffmann 1978).

There is also a difference now in the taxa constituting the Agriotheriinae.

Firstly, in the classification suggested here, *Ursavus depereti* is included in the Ailuropodini, since it is regarded as the likely ancestor of *Ailuropoda*. This means that it can no longer be referred to *Ursavus*, but must either be given a new generic name, or be referred to *Ailuropoda* itself. The latter course is favoured here, but in view of the uncertainties still surrounding this species neither of these alternatives is followed, and the doubtful generic identity of '*Ursavus' depereti* is indicated by quotation marks.

Secondly, if the Ursini, Tremarctini and Ailuropodini did, indeed, stem from the *Ursavus* group and are valid tribes, then the *Indarctos*-*Agriotherium* group of the Agriotheriini must be given the same status. This means that *Ursavus*, which is generally regarded as an agriotheriine (e.g. Kurtén 1966; HendeY 1972), has to be excluded from the tribe.

The various species of *Ursavus*, excluding '*Ursavus*' *depereti*, are accordingly placed in a new subfamily, the Ursavinae. Since this subfamily is not established on the same criteria as the others, it constitutes an unsatisfactory element in the classification as a whole. When their relationships are better understood, it may be possible to assign the species of *Ursavus* to other tribes, just as '*Ursavus*' *depereti* has been assigned to the Ailuropodini. The need for this additional subfamily will then fall away.

The classification of more primitive ursids, or ursid-like carnivores, namely, the hemicyonines and amphicyonines, was not investigated since they are largely irrelevant to the present study. They are mentioned here for the sake of completeness, but the conclusions regarding their status are tentative.

The Hemicyoninae are generally regarded as an early off-shoot of primitive ursid stock (probably *Cephalogale*—see Erdbrink 1953, fig. 61; HendeY 1972, fig. 1), and they are here included in the Ursidae.

The connection between the Amphicyoninae and later ursids is more remote, and the classification of this group is more controversial. They have been variously classified as a separate family (e.g. Hunt 1972), a subfamily of the Canidae (e.g. Kuss 1965), and as an ursid subfamily (e.g. Ginsburg 1977). The latter course is followed here.

The nomenclature of the species constituting the Agriotheriini is a far more problematical matter than the suprageneric classification of the Ursidae.

The conclusion that *Agriotherium* is directly descended from *Indarctos* with certain specimens exhibiting a combination of 'characteristics' of both genera, raises the possibility that they are congeneric, with *Agriotherium* the senior synonym. This situation had been foreseen even before *Indarctos* became well established in the literature (Pilgrim 1914; Merriam *et al.* 1916). It can be considered in relation to a similar situation involving the brown and polar bears.

Ewer (1973) and Van Valen (1978) have recently discussed the relative merits of opposing opinions on the generic identity of the polar bear. According to one widely held opinion the polar bear and brown bear are congeneric (i.e. both belong to the genus *Ursus*), while the opposing view is that the polar bear represents a separate genus (i.e. *Thalarctos*). Ewer and Van Valen favoured the latter alternative, a view which is supported here. A problem with this arrangement is that by one widely accepted criterion *Thalarctos* does not merit separate generic status. *Thalarctos maritimus* and *Ursus arctos* are known to produce fertile hybrids (see Van Gelder 1977). Van Valen (1978: 292) dismissed this objection in the grounds that 'lack of intersterility *per se*' is of 'low evolutionary importance' a fact for which Vrba (1979) has found supporting evidence amongst the Bovidae.

It is clear from their habitats and habits that *Thalarcos* and *U. arctos* are set on distinct evolutionary paths, and that given time they may well warrant generic separation by any standards. It is fortuitous that at present their divergence is not far advanced, although there is no doubt that this divergence does, in fact, exist. There will always be a problem in classifying species, both living and extinct, which are on separate lineages, but which are still close to a common ancestor. In instances where divergence is certain, and in the case of the brown and polar bears it is, then classification by 'clade' rather than 'grade' is preferable.

As indicated earlier, *Thalarcos* and *Agriotherium* are similar in the sense that both are essentially carnivorous forms derived from omnivorous ancestors. There is an apparent difference, however, in the evolutionary histories of these two genera. In the case of *Thalarcos* there was a divergence from the *U. arctos* group after which two lineages evolved independently, one with essentially carnivorous elements, and the other continuing with essentially omnivorous ones. In the case of *Indarctos*-*Agriotherium* it has been suggested above that the essentially omnivorous ancestor gradually adapted to give rise to the more carnivorous descendant forms and did not itself continue to exist as a separate entity. In other words, successive members of what may be regarded as a single lineage adapted their habits in response to a gradually changing environment (see p. 70).

This may, of course, be a misinterpretation of the fossil record and there may have been a dichotomy during the history of *Indarctos*-*Agriotherium* similar to that of *U. arctos*-*Thalarcos*. For example, Crusafont & Kurtén (1976) may be correct in their interpretation of the early history of *Indarctos*, and *I. vireti* may have given rise to both *I. arctoides* and the more *Agriotherium*-like *I. atticus*. According to this interpretation *I. vireti*-*I. arctoides* would be an equivalent of the *U. arctos* lineage, while *I. atticus* was the counterpart of *Thalarcos*. The nomenclatural implication is that *I. atticus* and other later *Indarctos* should be referred instead to *Agriotherium*, leaving only *I. vireti*, *I. arctoides* and the aberrant *I. anthracitis* as representatives of *Indarctos*. This arrangement is supported by the earlier suggestion that those species referred to throughout this report as 'advanced *Indarctos*', could as well be regarded as 'primitive *Agriotherium*'. A minor difficulty which arises is that *Indarctos* would have to be replaced by another name, because the genotype (*I. salmantanus*) would then be identified as an *Agriotherium*.

It could also be argued that since *I. vireti* is readily distinguishable from contemporary *Ursavus*, the evolutionary changes which were to culminate in *Agriotherium* were already being manifested early in the Vallesian. Thus *I. vireti* relative to contemporary *Ursavus* was the counterpart of the present-day situation involving *Thalarcos* and *U. arctos*. According to this interpretation all species presently identified with *Indarctos* should be referred instead to *Agriotherium*.

Both the above arrangements are less arbitrary than the existing one in

which it is only the most advanced agriotheriines which are referred to *Agriotherium*. This is unsatisfactory because it does not reflect the realities of the situation. Nevertheless, no changes in this arrangement are proposed here. Undescribed *Indarctos* and *Agriotherium* material from Asia and North America is available, and a decision regarding the status of these genera is best left until it, too, can be taken into account.

The same applies in the case of nomenclature at the species level, although some changes which reflect opinions on relationships are proposed here.

An appropriate starting point is with the European species, since they are amongst the best known and they represent the primary group from which agriotheriines elsewhere evolved. Four late Miocene species are recognized as valid. They are *I. vireti*, *I. arctoides*, *I. atticus* and *I. anthracitis*. *I. atticus* was apparently the first species to spread into Asia. *I. maraghanus* (De Mecquenem 1925) and *I. lagrelii* (Zdansky 1924) were apparently broadly contemporaneous with *I. atticus* and are here regarded as junior synonyms of this species.

The situation in respect of Siwaliks species is more problematical. The identifications of Pilgrim (1932), although regarded as unsatisfactory in some respects, are accepted here. Various possibilities will have to be considered in a revision of the Siwaliks material. For example, *I. punjabiensis* and *I. salmontanus* may represent a single species which is conspecific with *I. atticus*. Alternatively this species, or perhaps only *I. punjabiensis*, may be more advanced. The possibility that advanced Siwaliks *Indarctos* is conspecific with *A. palaeindicum* will also have to be considered. *A. sivalense* will be mentioned below.

Advanced *Indarctos* is also represented in Africa (Sahabi—see p. 73), and in North America, where material has been identified as *I. oregonensis* (e.g. Dalquest 1969), *I. nevadensis* (MacDonald 1959), or not identified as to species (e.g. Wolff 1978). There is no reason to believe that recorded North American *Indarctos* represents more than one species. Whether it should be identified as *I. oregonensis*, or referred to one of the Old World species, is not certain. The North American species was an immigrant from the Old World during the Hemphillian (Repenning 1967), and must, therefore, be closely related to a contemporary Asian species. It is here regarded as definitely distinct from *I. atticus*, but if *I. punjabiensis* is a valid species, it might be conspecific with, and the senior synonym of *I. oregonensis*.

Largely because of the uncertainties surrounding the Siwaliks species, *I. oregonensis* is here retained as a distinct species. In addition, the possibility was mentioned earlier that in certain respects North American *Indarctos* evolved independently of, and at a more rapid rate than its counterparts in Europe and Africa (see p. 82). If this were a development peculiar to North America, rather than both Asia and North America, then it would be another reason for recognizing *I. oregonensis* as a distinct species.

The situation in respect of recorded species of *Agriotherium* is complex, although the final solution with these species may be very simple. This solution, which is not advocated yet, is for all species of *Agriotherium* to be regarded as

junior synonyms of *A. sivalense*. Judged on the basis of the variation observed in the Langebaanweg *Agriotherium*, there may be no size or morphological grounds for recognizing more than one species of *Agriotherium*. However, it was decided to draw at least some distinctions on a geographical basis.

European *A. insigne*, which is here taken to include *A. intermedium* (Stach 1957), is tentatively regarded as valid. It was suggested earlier that African *Agriotherium* was an offshoot from the primary European lineage, and although *A. africanum* is almost indistinguishable from *A. insigne*, they are not regarded as conspecific, since the former is likely to be a descendant of north African *Indarctos* and was thus probably only indirectly related to European *A. insigne*.

There are some distinctive features in the dentitions of recorded *A. insigne* and *A. africanum* specimens which suggest that their phylogenetic connection may, indeed, have been indirect. For example, the European *A. insigne* specimen, NMB-MP549, has a double-rooted P^3 , a condition unknown in the Langebaanweg sample. On the other hand, no European specimen is known which has an 'intermediate cusp' on the P^4 protocone lobe or a vestigial M_1 metaconid, while none is known to lack the anterolingual cusp of M_2 . The possibility that European and African *Agriotherium* evolved independently will be discussed again below.

The situation in respect of *Agriotherium* in Asia and North America is similar to that with the *Indarctos* of these continents. *A. sivalense* is definitely a valid species, while *A. palaeindicum* is only tentatively regarded as such. Chinese *Agriotherium* is probably referable to *A. sivalense*. There is almost certainly only one species of *Agriotherium* represented in North America, and this may also be referable to *A. sivalense*. However, the North American species name which has priority, *A. schneideri* (Sellards 1916), is provisionally retained.

It has generally been assumed that North American *Agriotherium*, like *Indarctos*, was an immigrant from Asia (e.g. Repenning 1967). This is clearly a simple and logical interpretation of a situation where one genus supersedes another closely related one on a continent known to have received immigrants during the period in question. However, this is not the only interpretation possible. The fact that North American *Indarctos* includes some of the most *Agriotherium*-like specimens known suggests that the *Indarctos*-*Agriotherium* transition may have taken place in North America. If this were so then either the subsequent dispersal of *Agriotherium* started in North America, or *Agriotherium* evolved independently from advanced *Indarctos* in North America as well as in Europe and Africa.

The former alternative is unlikely in view of what is known of the Old World history of agriotheriines, whereas the independent evolution theory is a distinct possibility. This alternative appears to be implausible only in that it involves the polyphyletic origin of one genus as it is presently conceived. If, as indicated earlier, 'advanced *Indarctos*' is interpreted instead as 'primitive *Agriotherium*', it would mean that the *Indarctos*-*Agriotherium* transition took place once only (probably in Europe), and that once this evolutionary course

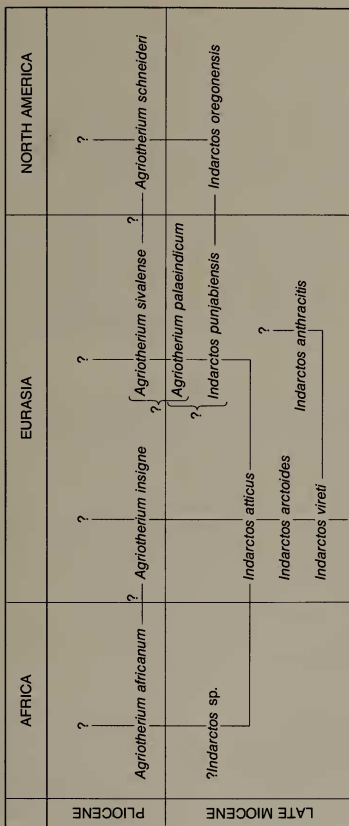


Fig. 42. A tentative arrangement of Agriotheriini in time and space.

had been set the development of *Agriotherium* (*sensu stricto*) could take place irrespective of the geographical location of the populations concerned.

Thus European *A. insigne* may have been descended from '*I. atticus*', *A. africanum* from the north African *Indarctos*-like agriotheriine, *A. sivalense* from the '*I. punjabiensis*/*A. palaeindicum* complex in Asia, while in North America '*I. oregonensis*' was ancestral to *A. schneideri*. It is nevertheless clear that there was a close connection between advanced agriotheriines in Europe and Africa on the one hand, and in Asia and North America on the other, and the above scenario may therefore be unrealistic. Instead *A. insigne* and *A. africanum* may share a common ancestor and be conspecific, while the same may apply to *A. sivalense* and *A. schneideri*. These alternatives are indicated in Figure 42. The possibility that all *Agriotherium* (*sensu stricto*) evolved from a single source is not favoured here, but it cannot yet be dismissed.

The nomenclature of this genus will ultimately have to be established by further testing of the hypotheses presented here, and perhaps by reference to conclusions reached in respect of other taxa with similar wide distributions and generally uniform characteristics. Amongst the latter are the living brown and black bears, as well as a wide variety of other carnivores, notably canids and felids.

SUMMARY

Available material of *Agriotherium africanum* from the latest Miocene/early Pliocene Varswater Formation at Langebaanweg is described. This species was found to be as variable as other bears of comparable size, this being in part due to marked sexual dimorphism.

The depositional environment and likely habitat and habits of the Langebaanweg *Agriotherium* are discussed. It is suggested that it was a large woodland carnivore, remains of which were transported to their points of discovery by a river which then met the sea in the vicinity of Langebaanweg. The transporting agent, and hyaenas, rodents, and fires contributed to the post-mortem damage exhibited by specimens.

Agriotherium was evidently descended from late Miocene *Indarctos*, the more significant evidence in support of this hypothesis being as follows:

1. There was an increase of size with time in the *Indarctos*-*Agriotherium* lineage, and advanced *Indarctos* may be little or no different in size to *Agriotherium*.
2. The skull characters of advanced *Indarctos* (e.g. *I. atticus* from Samos; *Indarctos* from Florida) are shared by *Agriotherium* (e.g. the Langebaanweg specimen L45062). Observable differences reflect further development of trends already evident in the *Indarctos* lineage. Significant shared characteristics are a relatively short and broad snout, with the posterior palatine incisure in line with the M² metacones, large zygomata and sagittal crest, and similar basi-cranial region, including absence of the alisphenoid canal.

3. There is little or no difference in the dentitions of advanced *Indarctos* and *Agriotherium*. For example, the incisors, canines, P₄'s, M₁'s, M₂'s and M₃'s may be morphologically indistinguishable. Differences that do exist reflect trends already evident in the *Indarctos* lineage. For example:

- (i) There was a progressive reduction in the size and number of anterior premolars in the *Indarctos*-*Agriotherium* lineage, with their principal cusps becoming progressively lower crowned and indistinct. However, *Agriotherium* sometimes has *Indarctos*-like upper premolars (e.g. *A. insigne*, NMB-MP549), while *Indarctos* may have *Agriotherium*-like lower anterior premolars (e.g. *I. atticus*, NMW-Samos 1912, 29).
- (ii) The shearing elements of the carnassials in the *Indarctos*-*Agriotherium* lineage are progressively developed, as are the buccal cusps of M₁ and M₂, which also have a shearing function. There is a corresponding reduction in the crushing elements of the posterior cheek teeth. For example, while the M₂ of *Indarctos* is distinguished from that of *Agriotherium* by the presence of a talon, this feature is progressively reduced in time. In advanced *Indarctos* it may be small (e.g. *I. punjabiensis*, GSI-D12), while vestiges of a talon may be present in *Agriotherium* (e.g. the Langebaanweg specimen L47698).
- (iii) As a general rule the P₄ of *Agriotherium* is distinguished from that of *Indarctos* by the presence of a parastyle, but this cusp may be present in advanced *Indarctos* (e.g. Samos *I. atticus*; most North American specimens).

4. A double-cusped P₄ protocone lobe is characteristic of European *Indarctos*, and is also found in some European and African *Agriotherium* specimens (e.g. *A. insigne*, NMB-MP549; Langebaanweg L2045 and others), although the P₄ antero-internal cusp is sometimes absent (e.g. *A. insigne*, Gervais (1859) specimen; Langebaanweg, L41404). The fact that this cusp is sometimes absent in *A. insigne*, and that in those specimens postdating L2045 it is reduced or absent, indicates that there was a tendency in European-African *Agriotherium* to lose the antero-internal cusp. A similar tendency is evident in advanced Asian and North American *Indarctos* (e.g. *I. punjabiensis*, GSI-D6; Florida *Indarctos*), while the antero-internal cusp is always absent in the *Agriotherium* from these continents. This common tendency in *Indarctos* and *Agriotherium* indicates a close relationship, while the examples cited suggest that the European/African and Asian/North American *Indarctos*-*Agriotherium* lineages evolved independently and at different rates later in their history.

The primary *Indarctos*-*Agriotherium* lineage was European and comprised *I. vireti*, *I. arctoides*, *I. atticus* and *A. insigne*, with *I. anthracitis* as an aberrant, probably island-dwelling offshoot. *Indarctos* emigrated to Africa, probably late in the Miocene, and an *Agriotherium* (*A. africanum*) very similar to the European *A. insigne* was evolved on this continent. Advanced *Indarctos* also migrated eastwards and the Asian/North American lineage is comprised of species of

Indarctos and *Agriotherium* postdating *I. atticus*. Pending further studies, most existing species names of these genera are retained.

It is suggested that either all *Indarctos*, or all later *Indarctos* (*I. atticus* and younger species) should be referred instead to *Agriotherium*, although the *status quo* is maintained for the present.

A modified suprageneric classification of later Ursidae is proposed. The species of *Ursavus* are included in a new subfamily, the Ursavinae. The Agriotheriinae are divided into two tribes, namely, Agriotheriini (*Indarctos*-*Agriotherium*) and the Ailuropodini (*'Ursavus'* *depereti*-*Ailuropoda melanoleuca*). The Ursinae and Tremarctinae are reduced to the status of tribes within a reconstituted subfamily Ursinae.

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